ORIGINAL ARTICLE

Fine-scale spatial patterns of the Tertiary relict *Zelkova abelicea* (Ulmaceae) indicate possible processes contributing to its persistence to climate changes

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Abstract   In this paper, the fine-scale spatial patterns of the Tertiary relict *Zelkova abelicea* (Lam.) Boiss. were studied (1) to reveal processes that contributed to its persistence to climate changes and (2) to assist future conservation planning, with the purpose of shifting the attention of conservation practitioners from patterns to processes. Results of the fine-scale spatial patterns of *Z. abelicea* indicate that the species tolerates disturbance and/or tracks changes resulting from disturbance in the range of its distribution through morphological and reproductive plasticity. In addition, our study indicates that *Z. abelicea* populations are conserved in the absence of metapopulation structure and that the species participates in plant–plant interactions through facilitation processes. Hence, the persistence of the species to climate changes seems to be more complicated and multifactorial than a linear and plain view of species survival in climate refugial areas, and therefore calls for a consideration of the processes revealed in this paper in future conservation planning.

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Introduction

Many extant plant species in current plant communities are
millions of years old and therefore have persisted through
dramatic changes in global climate, including the Neogene
climate fluctuations, the strong climate oscillations during
Quaternary, as well as the recent climate changes (Petit
et al. 2005). We know little regarding the ecological pro-
cesses that have allowed them to persist, while a large
number of model-based papers has been published on the
possible extinction of plant species due to the present cli-
mate change (cf. e.g., Thuiller et al. 2005; Malcolm et al.
2006). A majority of these models indicate alarming con-
sequences of climatic change for biodiversity, with some of
the worst scenarios postulating extinction rates that would
qualify as the sixth mass extinction in the history of earth
(Stork 2010; Barnosky et al. 2011; Bellard et al. 2012).

However, in some cases, the persistence of the above-
mentioned relict species can be at odds with the pessimistic
predictions of many model-based analyses of climate-dri-
ven range changes (Hampe and Jump 2011). Moreover,
species distribution models typically lack the spatial and
biological detail required to predict the persistence of
populations at the local level (Hampe and Jump 2011;
Schwartz 2012). This lack of detail may have significant
consequences on model output, even more so as fine-scale
biological and landscape characteristics as well as micro-
climate buffering have been demonstrated to play a central
role in species responses to climate change (Thuiller et al.
2008; Randin et al. 2009; Willis and Bhagwat 2009; Bar-
rows and Murphy-Mariscal 2012).

Zelkova abelicea (Lam.) Boiss. is such a relict species
(Tertiary relict) that has withstood long-range climate
changes and is restricted to the four main mountain ranges
in the island of Crete (Greece). Tertiary relict species are
defined here (see Denk et al. 2001) as extant species more
or less closely related to fossil taxa of different taxonomic
ranks (genus, section, species), which had relatively
extensive distribution ranges in western Eurasia during
different periods of the Cenozoic, but are at present con-
fined to small isolated relict areas.

The species belongs to the genus *Zelkova* which was
widespread in the Cenozoic. *Zelkova* appears to have been
part of humid mesic forests during the Miocene and Plio-
cene, but the deterioration of Cenozoic warm, moist cli-
mates during the Plio-Pleistocene resulted in the extinction
of the genus from many areas (Denk et al. 2001; Wang
et al. 2001). The oldest fossils attributed to the genus are

from the early Cenozoic (i.e., 55 Ma) of western North
America, where the genus is, however, extinct today
(Burnham 1986). The genus was widespread in Europe as
well; European fossils have mainly been ascribed to one
species, *Zelkova zelkovifolia* (Ung.) Bùzek et Kotl. (=*Z.
ungeri* Kov.). *Zelkova* in Europe became restricted to
refugia as the result of the cold and aridity during the
Pleistocene. Refugia, providing suitable habitats during
adverse climate periods, appear to have limited species
extinction as well as favouring the emergence of new taxa
(Médail and Diadema 2009). The genus eventually disap-
peared from continental Greece during the middle Pleis-
tocene (Van der Wiel and Wijmstra 1987), but persisted
longer in central Italy until ca. 31,000 BP (Follieri et al.
1986). The west Eurasian and east Asiatic taxa were
probably isolated starting in the middle Miocene as a result
of increasing aridity in central Asia (Wang et al. 2001).

In the present paper, we examine the spatial pattern of *Z.
abelicea* at a fine scale to (1) investigate processes that
could have contributed to the persistence of the species to
climate changes and (2) to investigate whether the results
of the spatial analysis could be incorporated in future
conservation planning, so as to shift the attention of con-
servation practitioners from spatial patterns to processes
(see Stein and Shaw 2013) that is to shift the attention from
conservation goals that focus on maintaining particular
spatial patterns in order to ensure that representative sam-
ples will survive in a specific area to process-oriented
goals, which focus on maintaining ecological processes
that, in turn, sustain the presence of species in the area.

Materials and methods

The species

Zelkova abelicea (Lam.) Boiss. belongs to the elm family
(Ulmaceae) is endemic to the island of Crete and is one of
the two European representatives of this otherwise Asiatic
genus (Fineschi et al. 2002, 2004). *Zelkova sicula*, rather
recently discovered in Sicily (Di Pasquale et al. 1992), is
the second Mediterranean species. Besides the two Medi-
terranean taxa, one species occurs in the Transcaucasian
and Hyrcanian regions (*Zelkova carpinifolia* (Pall.) K.
Koch) and three species are found in eastern Asia (*Zelkova
serrata* (Thunb.) Makino, *Zelkova schneideriana* Hand.-
Mazz. and *Zelkova sinica* C. K. Schneider) (Zheng-yi and
Raven 2003; Denk and Grimm 2005).

Zelkova abelicea is currently restricted to the four main
mountain ranges of Crete (Lefka Ori, Psiloritis—including
Kedhros, Dikti and Afendis Kavousi), at an altitudinal
range between 900 and 1,700 m a.s.l. The coordinates of
all known populations have recently been recorded

Fig. 1 Location of the study area in the East Mediterranean Region. Sites of known populations *of Z. abelicea* are indicated with *black dots*. *Contour line* 750 m
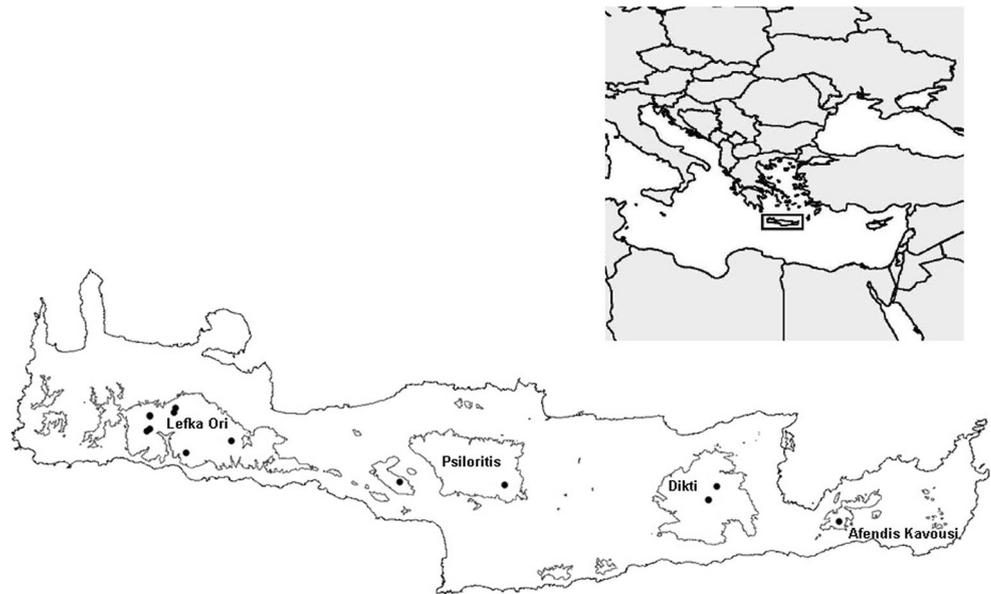
(Kozlowski et al. 2013), and the species has been classified as endangered according to IUCN criteria (Kozlowski et al. 2012).

The study area

Crete is the largest island of Greece and the fifth largest in the Mediterranean Basin, with a total surface of 8,729 km^2 and a west–east extension of about 254 km. Being one of the southernmost parts of Europe, it shares the same latitude with central Tunisia.

Calcareous rocks (limestone and dolomites) dominate the mountain terrain, whereas Neogene sediments, including limestones, sandstones and marls, cover large areas of the lowlands, along with ortho-quartzites, phyllites, flyschs, Quaternary rocks and alluvial deposits (Higgins and Higgins 1996).

The climate is Mediterranean with hot, dry summers and mild-to-cool, wet winters. Elevation and longitude have the largest influence on precipitation and yield the highest spatial correlation (positive to elevation and negative to longitude; Vrochidou and Tsanis 2012). Areal mean annual precipitation is estimated to 750 mm and varies from ca. 440 mm in the east (Ierapetra; 10 m a.s.l) to ca. 2,120 mm in the west (Askifou; 740 m a.s.l).

According to the NATURA2000 habitats classification scheme (European Commission 2007), Crete is dominated by *Sarcopoterium spinosum* phryganas, agricultures, *Olea* and *Ceratonia* forests, Dehesas, Mediterranean pine forests, *Cupressus* forests, endemic phryganas of the *Euphorbio-Verbascion* and endemic oro-Mediterranean heaths.

Data collection

Eleven of the 14 populations of *Z. abelicea*, described by Fazan et al. (2012), have been studied in this contribution; three have been omitted due to access restrictions related to the last heavy winter conditions.

Six populations have been sampled in the Lefka Ori Mountains, one in the Psiloritis Mountains (Rouvas Forest), three populations in the Dikti Mountains and one population in the Thripiti Mountains (see Online Resource 1). More details about the distribution of the island's *Zelkova* populations are presented in Fig. 1 and in Kozlowski et al. (2013).

For each population, two sampling sites have been selected. Data collection was performed with the line transect method (Elzinga et al. 1998) and included the sampling of one transect of 50 m per site. The only exception was Dikti Mountains, where 3 sampling sites have been selected for one of the three populations.

In this study, the line transect method was expanded to include detailed patch measurements. In addition to the projection of the canopy of each woody plant species on the line transect and the height of each plant, we performed measurements for each vegetation patch projected on the line transect. For each patch, we (1) recorded all woody species present at the patch (2) measured the maximum canopy length and the height of each woody plant species inside the patch (3) measured the maximum length and width of the patch, as well as the projection of the patch on the line transect. Abundance of species per patch was defined as the ratio of the cumulative projection of the canopies of each woody plant species to the projection of the respective patch on the line transect.

Conventionally, a distance of 0.5 m between the aerial parts of two neighboring plants was declared as the threshold beyond which two distinct patches can be identified.

In total, this study includes 268 vegetation patches projected on 23 line transects analyzed in 11 populations. Based on the height of the plants, we divided the records of Z. abelicea trees into 5 categories (see Online Resources 2–6 for details): (1) small shrubs (S1) with a height between 0 and 0.5 m; (2) intermediate shrubs (S2) ranging from 0.6 to 1 m; (3) large shrubs (M1) with heights between 1.1 to 2 m; (4) intermediate trees (M2) with heights of 2.1 to 3 m; and (5) large trees (L) being >3 m in height (and trespassing 10 m in several cases).

During fieldwork, we also investigated the occurrence of Z. abelicea seedlings and the mode of reproduction of Z. abelicea plants at the sampling sites to assess processes related to population turnover. In this regard, historical literature, herbarium records and recent observations covering the last 300 years (1700–2010; Kozlowski et al. 2013) have been used as well. Moreover, co-existing *Acer sempervirens* L. seedlings were recorded at the study site, annotating their position within and without shrubs and bushes of Z. abelicea.

Data analysis

A species distribution modeling approach has been applied at a coarser scale (0.6 × 0.6 km) to explore whether the current distribution of Z. abelicea fits the predictions of its probability distribution based on environmental predictors.

The coarse-scale distribution of Z. abelicea was predicted using MaxEnt, a maximum entropy-based machine learning program that estimates the probability distribution for a species' occurrence, based on the environmental constraints and its current occurrence data (Philips et al. 2006). The MaxEnt algorithm has been selected because it only requires present data for the study species, and it generally performs better than other modeling methods when working with small sample sizes (Pearson et al. 2007).

Records of the current position of Z. abelicea populations (15 points in total) were used as occurrence data for the model. For the selection of environmental predictors, the correlation of a broad set of environmental variables was measured by using a Pearson correlation coefficient. Environmental variables with a correlation coefficient of 0.7 or more were then excluded, resulting in a set of environmental variables (Table 1) which included topography, climate, land cover and soil characteristics.

The model was run, including all selected environmental variables (see Table 1 for details), using MaxEnt 3.3.3 through package *dismo* of the R statistical software (version 2.15.0; R Development Core Team, 2012). For evaluation purposes, the model was run following a fivefold

evaluation procedure. For each run, the data set was split into 80 % training and 20 % test data, and the area under curve (AUC) of the receiver operating characteristic (ROC) was estimated for test data. AUC values range from 0 to 1. Based on the literature, models with an AUC $\geq$ 0.7 are generally considered acceptable, models with an AUC $\geq$ 0.8 are considered excellent and models with an AUC $\geq$ 0.9 are considered outstanding (Hosmer and Lemeshow 2000).

At a finer scale, within its distribution, the co-occurrence of Z. abelicea with other species has been studied across different spatial scales. In this regard, we attempted to reveal whether community structure follows a nested pattern, i.e., whether the species composition of small assemblages is a nested subset of the species composition of larger assemblages (sensu Ulrich et al. 2009). Nestedness was quantified with the nestedness metric based on overlap and decreasing fill (NODF). Compared to other metrics (summarized by Ulrich et al. 2009), NODF has been described as unrelated to matrix characteristics such as matrix size or shape (Almeida-Neto et al. 2008). The significance of the results was determined with a Monte Carlo procedure (500 iterations) employing R0 null model (Wright et al. 1998). R0 has been selected among other null models, as a more intermediate choice with respect to the type I–type II error trade-off (Morrison 2013).

Since nestedness may fail to reveal underlying processes causing the observed patterns, it has been suggested that additional methods, such as gradient analysis, are used in combination (Ulrich et al. 2009). A two-way indicator species analysis (TWINSPAN; Hill 1979) has thus been applied to achieve a further ordering of sites and species. Analysis was conducted at different spatial scales and more specifically at three different hierarchical levels: (1) patch level (2) line transect level and (3) site level. At the patch level, TWINSPAN was run for all 268 sampled patches, as well as for all subsets of patches belonging to each of the 23 line transects and to each of the 11 sites. For the line transect and the site levels, species presences were pooled at the respective level, and TWINSPAN was run on the resulting matrices (23 × 15 and 11 × 15, respectively). Analysis was performed with the PC-ORD software (version 4.10; McCune and Mefford 1999).

Pairwise tests of species associations have been carried out using the method of Veech (2013). The probabilistic model of species co-occurrence allows to analytically (i.e., without randomization or simulation) obtain the probability that two selected species co-occur at a frequency either smaller or greater than the observed frequency of co-occurrence. The approach is not based on the use of a particular metric and randomization of the original data for the production of a p value, but is both distribution-free and metric-free. This probabilistic model does not rely on any

Table 1 Candidate variables for use in modeling of *Z. abelicea* distribution

Variable	Name description
Topographic variables	
alt[a]	Altitude
east[a]	Slope eastness
north[a]	Slope northness
slope[a]	Slope angle
Climatic variables	
rmean	Mean annual rainfall
rmax[a]	Maximum monthly rainfall
rmin[a]	Minimum monthly rainfall
tmean[a]	Mean annual temperature
tmax	Mean temperature of the hottest month
tmin	Mean temperature of the coldest month
Land cover variables	
bare[a]	Percent of pixel covered by bare soil
herbs[a]	Percent of pixel covered by herbaceous vegetation
trees[a]	Percent of pixel covered by trees
Soil variables	
s.AWC[a]	Available Water Storage Capacity
s.IL[a]	Impermeable layer
s.OR	Obstacles to roots
s.SCC	Subsoil Calcium Carbonate
s.SCECcl[a]	Subsoil cation exchange capacity for clay
s.SCECs	Subsoil cation exchange capacity for soil
s.SCLAY	Subsoil clay fraction
s.SGRAV[a]	Subsoil gravel content
s.SGYPS	Subsoil gypsum
s.SOC[a]	Subsoil organic carbon
s.SpH	Subsoil pH
s.SSAL	Subsoil salinity
s.SSAND	Subsoil sand fraction
s.SSILT	Subsoil silt fraction
s.SSOD[a]	Subsoil sodicity
s.STEB[a]	Subsoil total exchangeable bases
s.TCC	Topsoil Calcium Carbonate
s.TCECcl	Topsoil cation exchange capacity for clay
s.TCECs[a]	Topsoil cation exchange capacity
s.TCLAY	Topsoil clay fraction
s.TGRAV	Topsoil gravel content
s.TGYPS	Topsoil gypsum
s.TOC[a]	Topsoil organic carbon
s.TpH	Topsoil pH
s.TSAL	Topsoil salinity
s.TSAND[a]	Topsoil sand fraction
s.TSILT	Topsoil silt fraction
s.TSOD[a]	Topsoil sodicity

Table 1 continued

Variable	Name description
s.TTEB	Topsoil total exchangeable bases

Topographic variables were obtained from a Digital Elevation Model (DEM) originally produced by NASA, freely available at the website of the CGIAR cgiar-csi. Climatic variables were collected from the Hellenic National Meteorological Service (HNMS) and the Water Resource Department of the Prefecture of Crete (WRDPC). Land cover variables as collected by MODerate resolution Imaging Spectroradiometer (MODIS) sensor were downloaded from the Global Land Cover Facility website (http://glcf.umd.edu). Soil variables were retrieved from Harmonized World Soil Data Base (http://webarchive.iiasa.ac.at/Research/LUC/External-World-soil-database)

[a] Indicates that the variable was included in the model

data randomization; hence, it has a very low Type I error rate and is powerful since it also has a low Type II error rate. Nevertheless, taking into consideration the weakness of the probabilistic model in small data sets (Veech 2013), the classical chi-square method for species association has also been implemented.

Results

The probability distribution of *Z. abelicea* in the island of Crete, based on the model used, is presented in Fig. 2. This model seems to accurately represent existing conditions, as the points of occurrence of the species are in agreement with the areas of high probability of occurrence. This observation is also supported by the mean AUC results, which were 0.936. Moreover, this model may indicate that the current distribution of *Z. abelicea* on the island of Crete is not only driven by the climate variables investigated in this study, as climatic variables have a percentage contribution of only 2.1 %, whereas the other factors contribute with 97.9 % (Table 2).

Nestedness scores, calculated for different spatial scales, were significant ($p < 0.05$) for all hierarchical levels with the only exception of three lines at the patch level (LAS2-1, LAS2-2, NIA-2; Table 3). For all cases, NODF row-scores were higher than NODF column-scores, indicating that nestedness among species (i.e., species incidence) contributed more to the overall nestedness pattern than did nestedness among sites (i.e., species composition). This suggests that in the present case, differences in species associations are more important than differences in habitat variables of the sites in promoting nestedness. In other words, there are no sharp changes in species richness in a way that species assemblages in species-poor sites are

Fig. 2 Predictive output of MaxEnt for the model. *Darker areas* represent areas of higher probability of occurrence of *Z. abelicea*. Current occurrence *points* are indicated with *black dots with white outlines*
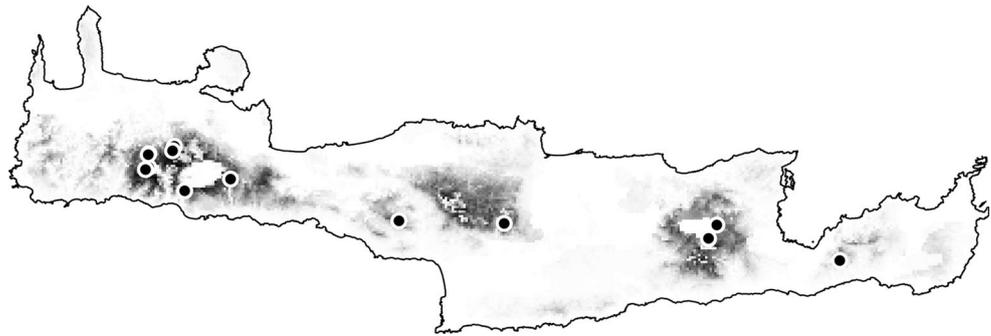
Table 2 Percent contribution of all variables used in the model, as estimated by MaxEnt

Variable	Percent contribution
alt	75 (74.62)
east	0 (0.02)
north	0 (0.2)
slope	1.6 (0.92)
rmax	0 (0)
rmin	0 (0.38)
tmean	2.1 (1.96)
bare	14.1 (11.68)
herbs	0 (0)
trees	0.1 (1.3)
s.AWC	0.1 (0)
s.IL	0 (1.16)
s.SCECcl	0.7 (0.48)
s.SGRAV	0.1 (0.28)
s.SOC	0 (0.02)
s.SSOD	4.7 (4.38)
s.STEB	1.3 (1.12)
s.TCECs	0 (0.96)
s.TOC	0 (0.4)
s.TSAND	0 (0)
s.TSOD	0.2 (0.1)

Numbers in parentheses indicate the mean contribution of the model that resulted from the fivefold evaluation procedure

subsets of those from more species-rich sites, but the relatively more rare species occupy a subset of the sites at which more widespread species are found.

This statement becomes even more evident in the TWINSPAN results presented in Tables 4 and 5, where table arrangement simultaneously took place in rows and columns. Noteworthy, a gradient analysis through clustering has been used as a supplementary approach for the identification of driving forces that cause nested subsets.

The role of species associations has also been further explored with a pairwise species approach for the three dominant forest tree species, *Z. abelicea*, *Acer sempervirens*

and *Quercus coccifera* L. Both the probabilistic and classical chi square approaches yielded identical results (Table 6). The non-significant relationship was the dominant pattern at the patch level in the two hierarchical scales, with only a few local exceptions of negative associations in the case of *Z. abelicea* and *A. sempervirens*. Nevertheless, by incorporating all patches at the island level in one data matrix, negative association was revealed for the pairs *Z. abelicea–A. sempervirens* and *Z. abelicea–Q. coccifera*, whereas positive association became apparent for the pair *A. sempervirens–Q. coccifera*.

Results on seedlings and the mode of reproduction of *Z. abelicea* plants in sampling sites are presented in Online Resource 1. No seedlings were recorded in the line transects under investigation and the dominant way of reproduction at the sites was vegetative through sprouting. In the Omalos area, *A. sempervirens* seedlings measured under *Z. abelicea* shrubs/bushes and out of *Z. abelicea* canopies revealed statistically significant differences (chi-square test, $p < 0.05$).

As compared to the historical records, the recent distribution of *Z. abelicea* (1993–2010) matches almost exactly the historical occurrences, and no dramatic shifts in distribution could be demonstrated for the past 300 years. However, several isolated populations, mainly in Lefka Ori and Psiloritis, appear to have gone extinct during the second half of the twentieth century (Kozlowski et al. 2013), and new populations could not be discovered during recent field investigations.

At the finer scale (patch level), *Z. abelicea* had a relative frequency of 73.51 %, which was unequally distributed in the different categories, with tree categories (intermediate-M2 and large trees-L) presenting the lowest values.

Furthermore, several patterns of relationships between patch size and other parameters become evident; one such is the absence of any correlation between the sizes of patches and the number of species comprised in it (Fig. 3). Moreover, a statistically significant negative correlation was found between the abundance of each *Z. abelicea* shrub form and the logarithm of the patch size ($R^2 = 0.6568$, 0.4911 and 0.5743 for small, intermediate

Table 3 Results of nestedness tests based on the R0 null model

Data set	Fill	NODFcolumns	NODFrows	NODF
All patches	0.151	28.03 (+)	47.52 (+)	47.46 (+)
All lines	0.371	56.74 (+)	70.15 (+)	66.22 (+)
All sites	0.412	55.94 (+)	64.97 (+)	59.05 (+)
LAS1_1	0.173	5.24 (−)	57.04 (+)	20.78 (+)
LAS1_2	0.213	11.31 (−)	65.56 (+)	27.58 (+)
LAS1_3	0.233	5.08 (−)	35.56 (+)	8.89 (−)
LAS2_1	0.164	5.52 (−)	40.61 (+)	17.58
LAS2_2	0.225	10.48 (−)	77.68 (+)	24.62
LAS3_1	0.161	3.54 (−)	65.15 (+)	27.32 (+)
LAS3_2	0.2	10.24	68.89 (+)	17.57 (+)
NIA_1	0.11	2.86	32.97 (+)	16.84 (+)
NIA_2	0.21	8.41 (−)	69.84 (+)	18.65
OMA1_1	0.113	4.83	42.22 (+)	16.04 (+)
OMA1_2	0.072	0.48	7.69 (+)	3.55 (+)
OMA2_1	0.089	1.43	43.94 (+)	17.84 (+)
OMA2_2	0.125	1.95	60.71 (+)	14.32 (+)
OMA3_1	0.129	10.55	48.02 (+)	29.28 (+)
OMA3_2	0.171	10.45 (−)	68.96 (+)	37.61 (+)
OMA4_1	0.147	11.35	51.43 (+)	31.39 (+)
OMA4_2	0.118	4.56	25 (+)	13.27 (+)
PSI_1	0.171	12.97	59.43 (+)	34.54 (+)
PSI_2	0.152	9.15 (−)	63.37 (+)	34.32 (+)
STA_1	0.174	12.22	69.23 (+)	36.52 (+)
STA_2	0.19	5.9 (−)	59.62 (+)	28.8 (+)
AMB_1	0.107	1.71 (−)	53.33 (+)	27.52 (+)
AMB_2	0.164	6.98 (−)	69.21 (+)	38.1 (+)
AMB	0.136	5.77 (−)	63.03 (+)	51.89 (+)
LAS1	0.203	10.46 (−)	47.59 (+)	38.52 (+)
LAS2	0.189	9 (−)	58.04 (+)	39.38 (+)
LAS3	0.174	8.85 (−)	58.82 (+)	38.48 (+)
NIA	0.143	8.81 (−)	44.84 (+)	32.83 (+)
OMA1	0.09	3.07	24.11 (+)	17.94 (+)
OMA2	0.103	1.79 (−)	49.47 (+)	32.5 (+)
OMA3	0.149	12.49 (−)	57.41 (+)	48.18 (+)
OMA4	0.133	10.3	37.57 (+)	31.64 (+)
PSI	0.162	13.43 (−)	60.07 (+)	49.93 (+)
STA	0.182	10.86 (−)	59.74 (+)	47.81 (+)

(+) Observed NODF is statistically significantly higher than that expected by chance (high nestedness)

(-) Observed NODF is statistically significantly lower than that expected by chance (low nestedness)

"All patches" row refers to a matrix created by all 268 patch data, "all lines" refers to pooled presence data for the 23 line transects and "all sites" refers to pooled presence data for the 11 sites. Individual site matrices are coded based on population (see Table S1), while individual line transect matrices are coded in the format S_L, where S is the site code and L the index of the line transect. "Fill" refers to the total fit of the matrix. Columns "NODFcolumns" and "NODFrows" refer to the NODF as measured only according to matrix columns and rows, respectively, while "NODF" refers to the total NODF

and large shrub forms respectively; $p < 0.01$ in all cases) (Fig. 4a–c). Such a trend was not maintained in the tree forms (Fig. 4d), where no correlation was found.

As far as the co-occurrence of *Z. abelicea* with other species is concerned at the patch level, increasing numbers of species co-occurring with *Z. abelicea* resulted in a decrease of the number of patches where co-occurrence is recorded (Fig. 5a).

The same trend appears when correlating the number of co-occurring species with the abundance of *Z. abelicea* per patch (Fig. 5b). The deviation in the case of 5 species is presumably reflective of the low number of available patches.

When exploring the co-occurrence of *Z. abelicea* categories in patches, it also becomes obvious that many patches (171) with shrub category occurrences (small, intermediate and large shrubs) will be void of intermediate and large trees. We only identify three patches where the intermediate and the large trees co-occur or occur in the absence of shrubs. A chi-square test of the contingency table of *Zelkova* shrubs and trees showed a statistically significant deviation from the expected by chance frequencies. Specifically, intermediate and large trees were found less frequently than expected.

Discussion

In the case of the extant Mediterranean flora, many ancient taxa evolved during the Cenozoic, well before the typical Mediterranean climate regime was established (Pulido et al. 2008). A number of Tertiary relict taxa evolved from lineages that thrived under warm temperate (fully humid or winter dry) climates during most parts of the Cenozoic. Examples of Tertiary relict taxa that are at present confined to the Mediterranean region are, among others, *Platanus orientalis* L., *Liquidambar orientalis* Mill., *Z. abelicea* and *Z. sicula*. In contrast to the Cenozoic climate, today, these taxa have to cope with summer dry and hot conditions typical of the Mediterranean climate. As a result, these climate relict trees invariably exhibit highly fragmented ranges and low population sizes in southern Europe (Pulido et al. 2008). *Zelkova abelicea* is such a relict species, persisting in a few sites in the island of Crete.

Probability of occurrence and biotic interactions

In this study, the low explanatory contribution of the climatic variables in the model indicates that the current distribution of *Z. abelicea* on the island of Crete may not be driven by climate alone, but that other factors may play a central role. Of course, we are well aware that the model is strongly depending on the choice of climatic

Table 4 Results of the two-way indicator species analysis on the line matrix (each column represents a line transect)

	OMA1_1	OMA3_1	OMA3_2	OMA4_1	OMA4_2	LAS1_2	PSI_1	LAS1_1	LAS1_3	LAS2_1	LAS2_2	LAS3_1	LAS3_2	NIA_1	OMA1_2	PSI_2	STA_1	STA_2	OMA2_1	OMA2_2	AMB_1	AMB_2	NIA_2
CraMon	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RhaOle	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RhaAla	-	1	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
QueCoc	1	1	1	1	1	1	1	1	1	1	1	-	1	1	1	1	-	-	-	-	-	-	-
ZelAbe	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
EupAca	-	1	1	1	1	1	1	1	1	1	1	1	1	1	-	1	1	1	-	-	1	1	1
BerCre	1	1	1	1	1	1	1	1	1	1	1	-	-	1	-	1	1	1	1	1	1	1	1
AceSem	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	1	1	1	1	1
DapSer	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
SarSpi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Teu	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
PhlCre	-	-	-	-	-	1	1	-	1	1	1	1	1	-	-	1	1	1	-	-	-	-	-
PhlLan	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
VerSpi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
PruPro	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1

Value 1 indicates presence of the according species to that particular line transect, while horizontal dashes (–) indicate absence. Double lines delimit the groups that resulted from the first division and single lines delimit the groups that resulted from the second one

Species abbreviations: *AceSem Acer sempervirens*, *BerCre Berberis cretica*, *CraMon Crataegus monogyna*, *DapSer Daphne sericea*, *EupAca Euphorbia acanthothamnos*, *PhlCre Phlomis cretica*, *PhlLan Phlomis lanata*, *PruPro Prunus prostrata*, *QueCoc Quercus coccifera*, *RhaAla Rhamnus alaternus*, *RhaOle Rhamnus oleoides*, *SarSpi Sarcopoterium spinosum*, *Teu Teucrium sp*, *VerSpi Verbascum spinosum*, *ZelAbe Zelkova abelicea*

Table 5 Results of the two-way indicator species analysis on the line matrix (each column represents a site)

	NIA	OMA1	OMA3	OMA4	LAS1	PSI	LAS2	LAS3	AMB1	OMA2	STA
PruPro	1	-	-	-	-	-	-	-	-	-	-
VerSpi	1	-	-	-	-	-	-	-	-	-	-
RhaAla	-	-	1	1	1	1	-	-	-	-	-
RhaOle	-	-	1	1	-	-	-	-	-	-	-
CraMon	-	1	-	1	-	-	-	-	-	-	-
QueCoc	1	1	1	1	1	1	1	1	-	-	-
AceSem	1	1	1	1	1	1	1	1	1	1	1
BerCre	1	1	1	1	1	1	1	-	1	1	1
EupAca	1	-	1	1	1	1	1	1	1	-	1
ZelAbe	1	1	1	1	1	1	1	1	1	1	1
PhlCre	-	-	-	-	1	1	1	1	-	-	1
Teu	-	-	-	-	-	-	-	1	-	-	-
SarSpi	-	-	-	-	-	-	-	-	-	-	1
DapSer	-	-	-	-	-	-	-	-	-	-	1

Value 1 indicates presence of the according species to that particular line transect, while horizontal dashes (–) indicate absence. Double lines delimit the groups that resulted from the first division and single lines delimit the groups that resulted from the second one. Species abbreviations as in Table 4

variables, but a minimum set of available parameters have been chosen to avoid overfitting, which in turn may result in artifacts (Beaumont et al. 2005; Heikkinen et al. 2006; Araújo and Peterson 2012). The fact that the total contribution of the direct abiotic variables (i.e., soil, landscape and climate variables) in the model reaches 10.8 %, whereas bare soil and plant cover attain 14.1 and 0.1 %, respectively, also indicates that patterns resulting from disturbance and biotic interactions may also be important. Besides, altitude, which is the highest contributing variable in the model (75 %), as an indirect variable may also comprise biotic interactions and partially may reflect non-selected climatic variables.

These results depict a scenario partially different as referred to the closest biogeographical and ecological relative *Z. sicula*, particularly with concern to the role of certain abiotic factors such as available water storage capacity in the soil. Actually, the current distribution of the Sicilian species is suggested to be strictly depending on underground water resources, since both known populations are essentially restricted to the bottom of thalwegs (Garfì et al. 2011). This situation has been interpreted as an adaptive strategy or a refugial persistence allowing the species to face the constraints of summer water stress typical of Mediterranean climate. According to that, besides palaeoecological data (cf. Béguinot 1929; Follieri

Table 6 Results of the pairwise association tests using chi-squared tests and the probabilistic method of Veech (2013)

	chi squared			Probabilistic		
	Z-A	Z-Q	A-Q	Z-A	Z-Q	A-Q
All patches	−	−	+	−	−	+
LAS1_1	0	0	0	0	0	0
LAS1_2	0	0	0	0	0	0
LAS1_3	0	0	0	0	0	0
LAS2_1	0	0	0	0	0	0
LAS2_2	0	0	0	0	0	0
LAS3_1	0	0	0	0	0	0
LAS3_2	0	0	0	0	0	0
NIA_1	0	0	0	0	0	0
NIA_2	0	0	0	0	0	0
OMA1_1	0	0	0	0	0	0
OMA1_2	−	0	0	−	0	0
OMA2_1	0	0	0	0	0	0
OMA2_2	0	0	0	0	0	0
OMA3_1	0	0	0	0	0	0
OMA3_2	0	0	0	0	0	0
OMA4_1	0	0	0	0	0	0
OMA4_2	0	0	0	0	0	0
PSI_1	0	0	0	0	0	0
PSI_2	0	0	0	0	0	0
STA_1	0	0	0	0	0	0
STA_2	0	0	0	0	0	0
AMB_1	0	0	0	0	0	0
AMB_2	0	0	0	0	0	0
LAS1	0	0	0	0	0	0
LAS2	0	0	0	0	0	0
LAS3	−	0	0	−	0	0
NIA	0	0	0	0	0	0
OMA1	−	0	0	−	0	0
OMA2	−	0	0	−	0	0
OMA3	0	0	0	0	0	0
OMA4	0	0	0	0	0	0
PSI	−	0	0	−	0	0
STA	0	0	0	0	0	0
AMB	0	0	0	0	0	0

In columns, pairs of the three species *Z. abelicea, A. sempervirens* and *Q. coccifera* are denoted by pairs of the letters Z, A and Q, respectively. Matrix codes are the same as in Table 3

0 No statistically significant association detected

+ Statistically significant positive association detected (p value < 0.05)

− Statistically significant negative association detected (p value < 0.05)

et al. 1986; De Paola et al. 1997) and observations on exceptional performances of a few cultivated trees (Garfì, unpublished), a more humid environment as is found at
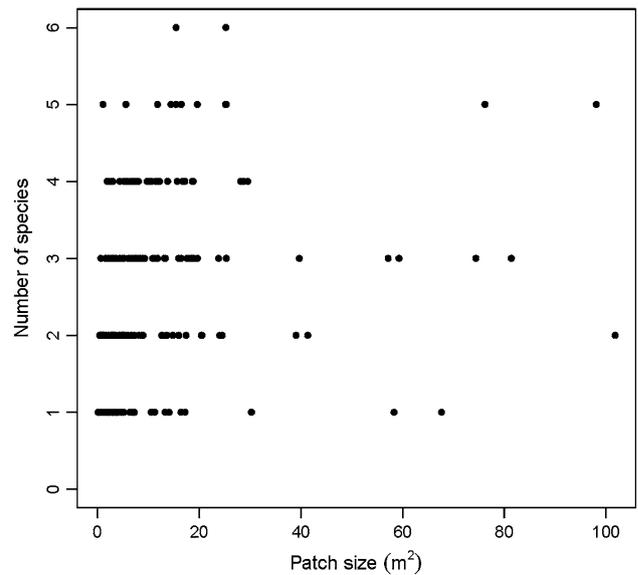
Fig. 3 Patch size in square meters and the number of species comprised in it. *Each point* represents a single patch out of the 268 sampled

higher elevation (e.g., supra-Mediterranean or montane forest habitats dominated by *Fagus, Acer, Carpinus, Taxus,* deciduous-type *Quercus,* etc.) is inferred to better match with the ecological requirements of *Z. sicula* (Garfì and Buord 2012). Such an assumption could be somehow consistent with the main results of distribution modeling of *Z. abelicea*, showing the overwhelming significance of altitude in affecting the species persistence.

Even though biotic interactions have generally been considered to be unimportant in determining large-scale distributions (for a review see Wisz et al. 2013), they have recently been suggested to affect species distributions and plant assemblages at regional, continental and global scales (Hampe and Jump 2011; Wisz et al. 2013). Thus, biotic interactions ought to be considered in management practices of *Z. abelicea*.

The possible role of biotic interactions is also supported by the fact that nestedness among species contributed more to the overall nestedness pattern than did nestedness among sites. According to Ulrich et al. (2009), nestedness is a pattern of species co-occurrence, intrinsically related to the degree of species aggregation, and the correlation between nestedness and co-occurrence metrics might be used to identify non-random species associations.

At the line and at the site level, the results of the TWINSPAN approach strengthen the above findings, revealing that *A. sempervirens* and *Z. abelicea* are widespread in all lines and sites, along which species loss and species replacements take place among the remaining species. However, a divergence from this pattern is observed at the patch level, where the two species seem to
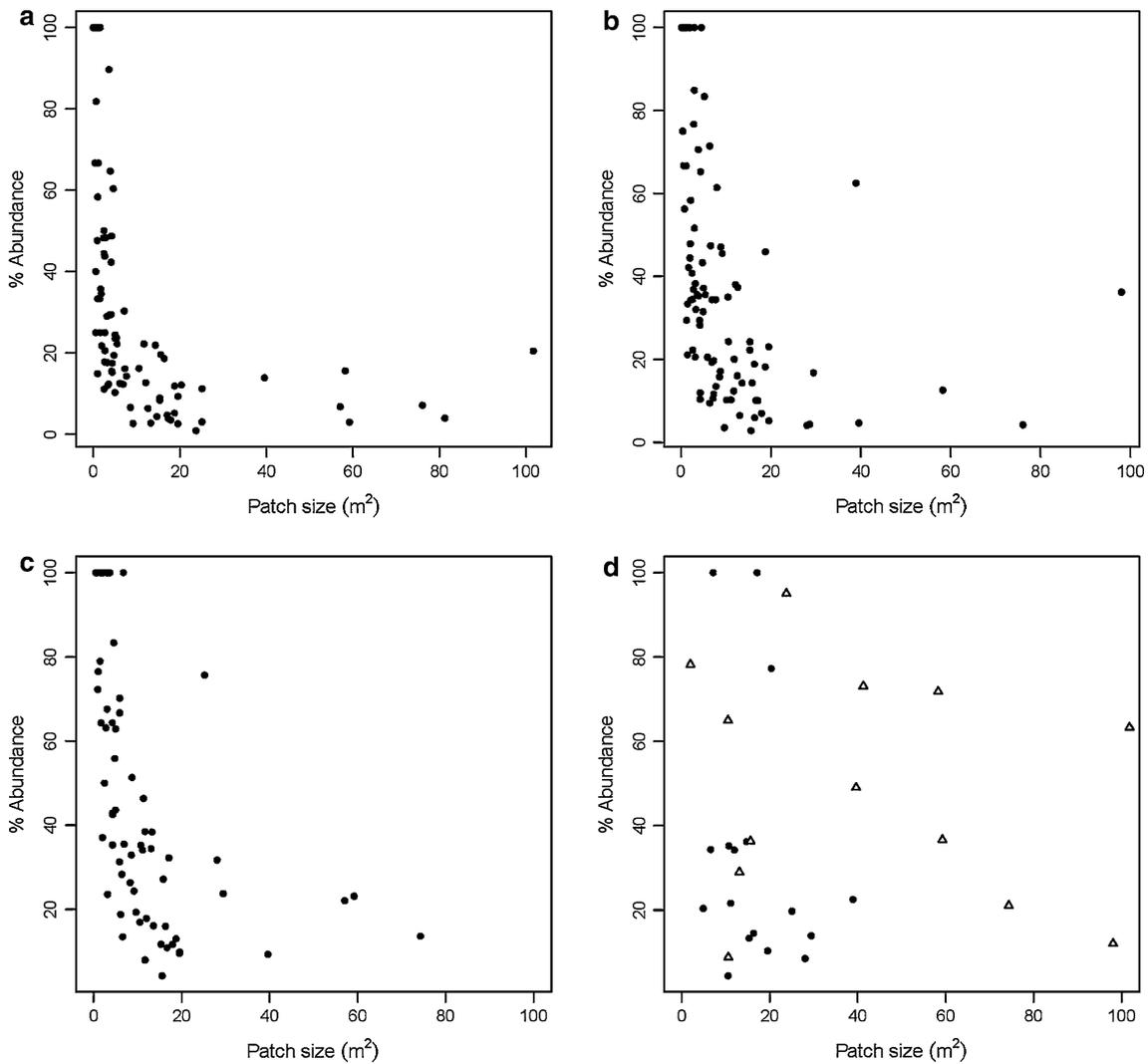
Fig. 4 Relationship between patch size in square meters and percent relative abundance of each *Z. abelicea* form: S1 (**a**), S2 (**b**), M1 (**c**), M2 (**d**, *black dots*) and L (**d**, *white triangles*). Codes are in accordance with "Materials and methods"

Fig. 5 Frequency of the number of species co-occurring with *Z. abelicea* in each patch (**a**) and its relationship with the patch abundance of *Z. abelicea* (**b**). In (**b**), *boxes* are 0.25 and 0.75 quantiles and medians, while *whiskers* are 1.5-fold interquantile range
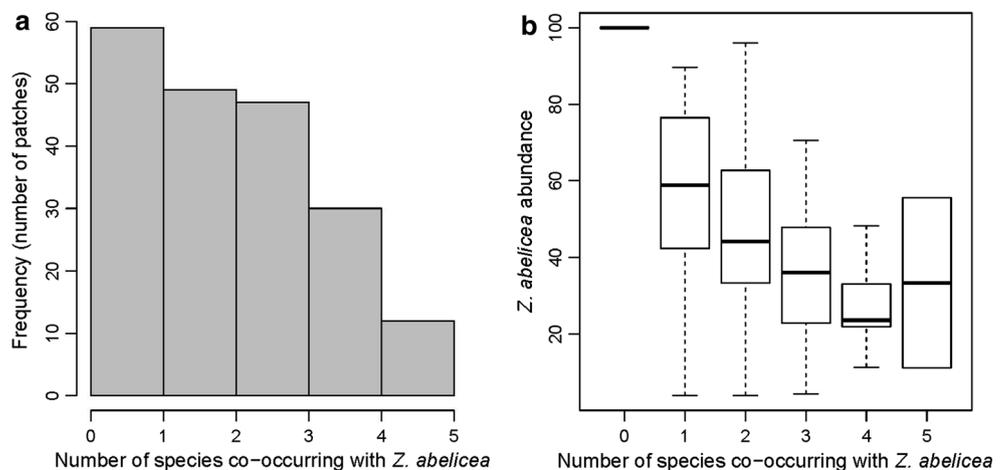
be distributed independently, as also supported by the non-significance of the pairwise species association metrics.

Although this may seem contradictory at first, it may be related to different driving forces, which determine patterns at the different hierarchical levels. For example, *Z. abelicea* and *A. sempervirens* may exhibit positive interactions at the site and line levels, which diminish at the patch level. This is in line with their co-occurrence according to nestedness and TWINSPAN results at these levels and is consistent with the differentiated pattern at the patch level.

By positive interaction, we mean a situation where the presence of one species modifies the environment in ways that reduce some physical disturbance or stress, so that less tolerant species perform better. Facilitation is the most frequent plant–plant interaction in stressful environments (Bertness and Callaway 1994; Callaway et al. 2002; Gómez-Aparicio et al. 2004), where facilitator species can improve conditions to the benefit of other species.

In our case, a possible positive interaction between *Z. abelicea* and *A. sempervirens* could be related to the hydraulic redistribution of water in the soil (Brooksbank et al. 2011), a process which describes transport of water via roots along water potential gradients from wetter to drier parts of the soil profile. This usually occurs nocturnally, when reduced transpiration results in the root water potential in dry soil layers rising above the water potential of the surrounding soil.

Hydraulic redistribution has been shown to add in some cases the equivalent of 0.7 mm day^{-1} of water to the upper 1 m of soil (Scholz et al. 2010), and the phenomenon has been largely investigated for *Acer saccharum* (Stoll and Weiner 2001). During drought periods, *Acer saccharum* demonstrates "hydraulic lift," a nocturnal uptake of water by roots from deep soil layers that is released from shallow roots into upper soil layers (Dawson 1993), so that neighboring plants can use 3–60 % of the hydraulically lifted water supplied by *Acer saccharum* trees. Overall, hydraulically redistributed water has been shown to increase annual water use in *A. saccharum* forest by 19–40 % (Caldwell et al. 1998).

Consistently, although no specific measurements have been carried out in this study, we hypothesize that in such a positive interaction between *Z. abelicea* and *A. sempervirens*, *Acer* possibly contributes to the hydraulic redistribution, through "hydraulic lift." Our assumption is in agreement with Valiente-Banuet et al. (2006) who reported that a large number of Tertiary relict species in Mediterranean climate ecosystems appear to have been preserved by the facilitative effects of other species. Nevertheless, whether *A. sempervirens* is a modern Quaternary plant lineage is not clear. Although an adaptive shift of *A. sempervirens* to the Mediterranean climate,

accompanied with increased mutational activities, could have occurred in the Pleistocene (Grimm et al. 2007), the "Quaternary species hypothesis" is still controversial for *A. sempervirens*. Our assumption also suggests that *Z. abelicea* would belong to the category of biotically sustained (BS) relicts (Hampe and Jump 2011), i.e., species that requires for its persistence a mutualist that is also limited by climate.

Along this line of thoughts, any conservation practice addressed to the removal of *A. sempervirens* trees from the ecosystem in benefit of *Z. abelicea* should carefully consider the dependence of the latter on the presence of the first. Further research is clearly and critically needed to explore these plant–plant interactions over all ranges of species co-occurrence, as the initial facilitation between species can shift into competition at a certain ontogenetic stage (Valladares 2008). This ontogenetic shift may help to reconcile contrasting results on facilitation versus competition outcomes on plant–plant interaction in dry ecosystems.

Additional positive interactions, such as the nursing role of *Z. abelicea* to the establishment of *A. sempervirens* seedlings, cannot be excluded. According to our field observations, significantly more *A. sempervirens* seedlings are found under *Z. abelicea* shrubs than in open areas or under other species. This nursing behavior could be related to the protection of *A. sempervirens* seedling from grazing, high radiation, wind, low temperatures and/or to the preservation of soil water and nutrients. This observation is in agreement with other studies where *Acer* saplings have been demonstrated to need the protection of nurse species (Gómez-Aparicio et al. 2005; Quero et al. 2008). Species such as *Sorbus* or *Quercus* spp. have been observed to establish better under shrub canopies as well, owing to the lacking ability of seedlings and saplings to withstand high radiation (Mendoza et al. 2009) or to the shelter role played by shrubs against animal browsing (Di Pasquale and Garfi 1998). Nevertheless, in order to support such a hypothesis about a possible nursing role of *Z. abelicea*, more research, measurements and experiments will be needed.

On the other hand, the lower frequency of co-occurrence between *Z. abelicea* and *Q. coccifera* prompts different assumptions. Although the relationship between *Z. abelicea* and *Q. coccifera* is unknown at the moment, it may possibly be linked to the lower tolerance of *Z. abelicea* to dryness and disturbance, as compared to *Q. coccifera*. The latter is generally well known for its high degree of physiological and morphological plasticity (Valladares et al. 2002). This hypothesis is also in support of the assumption of the supposed dependence of *Z. abelicea* on the "hydraulic lift." Moreover, the distribution of *Q. coccifera* is mostly limited to the dry, higher parts of dolines in the present case and further supports this hypothesis.

Disturbance and population structure

Focusing on the patches, the absence of correlation between the size of a patch and the number of species it contains seems analogous to the observations recorded by Gavilán et al. (2002) in Spain. The question arising here is whether disturbance, especially grazing, could be invoked in the explanatory framework of the absence of correlation. The participation of bare soil as an explanatory variable in the full model with a contribution of 14.1 % seems to be in strong support of such an assumption.

In fact, disturbance has been demonstrated to influence species richness (Mackey and Currie 2001), and several hypotheses have been proposed for the diversity–disturbance relationship. The intermediate disturbance hypothesis (IDH) (Levin and Paine 1974; Connell 1978) can be seen as the leading hypothesis for this relationship, whereas empirical evidences reviewed in Proulx and Mazumder (1998) suggest that this relationship would depend on the productivity of the ecosystem. IDH predicts small and large species numbers at low or high/intermediate levels of disturbance, respectively, and this independently of patch size.

Additionally, in case the dominant species is the one mainly affected by disturbance pressure both in large and small patches, the number of participating species in the patches is increasing. Yet, when the dominant species escapes disturbance or, on the contrary, disappears from the area due to disturbance pressure, the pressure is redirected to the non-dominant species. The number of participating species in the patches will thus be decreasing, leading to a small number of species independent of the patch size. In any case, diversity–disturbance relationship in both patch sizes can be either negative or positive depending on the intensity of disturbance as well as on the productivity of ecosystem, leading to a small or a large number of species.

As an outcome of the above, it can be assumed that the absence of correlation between species number and patch size, incorporating all the patches of the sites investigated in this study, may be related to multiple disturbance, especially grazing aspects (in terms of frequency and intensity) and their interactions, which usually cause mosaic disturbance patterns.

Consequently, as the persistence of Z. abelicea does not only seem to be a matter of isolated enclaves in suitable climatic areas, other disturbances and more specifically herbivory should be considered as a prominent factor influencing the response of Z. abelicea. Herbivory should therefore be considered in conservation planning as well, mainly by promoting controlled grazing as a management tool in some selected cases rather than favoring their complete removal by fencing. Generally, morphological and reproductive plasticity could possibly represent an advantageous strategy to track changing conditions due to disturbance, in particular mosaic disturbance (Valladares and Gianoli 2007; Keppel et al. 2012) which characterizes Mediterranean refugia, and further facilitate resistance to climate change in highly variable environments (Richter et al. 2012). Noteworthy in this context, fencing of the Psiloritis population (Rouvas forest) has proven unsuccessful as heavy snow has partially destroyed the fences, and as local shepherds do not prevent their animals from entering fenced areas.

Nevertheless, despite the absence of the above correlation between patch size and number of species occurring per patch, Z. abelicea abundance per patch seems to be decreasing as the number of other species per patch increases (Fig. 5b). This finding could partially be explained by the fact that A. sempervirens is the dominant and widespread tree species in the selected sites and, as a consequence, a reduction in its abundance due to grazing and/or browsing would lead to the increase in the number of other co-occurring species per patch. This is not, however, the case of Z. abelicea abundance per patch, which in contrary to the other woody species is negatively influenced by the reduction in A. sempervirens. In addition, this finding might also be reflective or indicative of a weak competitive ability of Z. abelicea against other woody species.

Still regarding patch size, the inverse correlation between the abundance of Z. abelicea shrubs and patch size is in opposition to a pattern where high and low abundances of tree habits can indifferently be observed in both small and large patches. Fazan et al. (2012), demonstrated that severely browsed Z. abelicea trees, while often remaining very small, can attain high ages (>500 years) and thereby greatly surpass in age large, normally growing neighboring trees. It can thus be suggested that the different populations do not represent different successional stages, with shrubs at the first and trees at the following stages. Rather, tree habit seems to be the result of escape from grazing and independent of succession. This concept is further supported by the fact Z. abelicea trees do not seem to form continuous and exclusive forests at the studied sites, but that they occur in mixed forests with A. sempervirens and Q. coccifera (Egli 1997; Søndergaard and Egli 2006). Additionally, paleobotanical evidence showed the co-occurrence of Zelkova species with evergreen oaks and other species (Follieri et al. 1986, 1989; Boyd 2009). Therefore, any restoration efforts for Z. abelicea (e.g., reforestation for the formation of single species stands) should take this aspect into account (see also Godefroid et al. 2011; Loss et al. 2011).

By taking into consideration coarse- and fine-scale results, a matter of scale appears (Levin 1992) and an additional question arises—whether the persistence of

Z. abelicea is the result of bottom-up processes, where processes at a lower hierarchical level determine the dynamics at a higher level (Jeltsch et al. 2008) or the result of top-down processes. In other words, the issue is whether the current distribution of spatially structured Z. abelicea populations in Crete is defined by ecological processes taking place at the patch level (bottom-up) or if persistence at the patch level is defined by ecological processes at the broader area level (top-down).

In a metapopulation context, despite the reduction in relative frequency at the patch level, persistence is possible if re-colonization exceeds extinction (Hanski 1991). However, in the investigated patches, young seedlings could not be recorded and vegetative propagation was the only visible way of reproduction for the shrubby plants of Z. abelicea, which exhibit extremely higher frequencies compared to the tree forms. Interactions between populations clearly are an essential prerequisite of metapopulation processes, but such a structure does not seem to be present in the case of Z. abelicea.

Nevertheless, we cannot exclude interactions between some of the Z. abelicea populations in Lefka Ori, where fruiting, though limited, was observed in Z. abelicea large trees (Fazan et al. 2012), but the absence of Z. abelicea young seedlings, even in these populations, clearly diminishes the likelihood of such occurrences. Thus, the population structure of Z. abelicea seems to follow the "regional ensembles" pattern, in which local processes are dominant; long-range colonization through dispersal is rare or absent and where local populations are basically unconnected at a regional scale (Freckleton and Watkinson 2002).

Further evidence for the lack of metapopulation structure lies in the historical records of Z. abelicea distribution for the last 300 years (Kozlowski et al. 2013), according to which no population shifts have occurred. As a consequence, it could be hypothesized that bottom-up processes, mainly related to the persistence by forceful vegetative reproduction of Z. abelicea, are regulating the regional distribution and abundance of Z. abelicea populations and that processes at the patch level should be taken into consideration for conservation planning (Freckleton and Watkinson 2002). On the other side, this is not the case for other relict species, such as Liquidambar orientalis, where a metapopulation structure has been reported (Öztürk et al. 2008). One possible conclusion might thus be that conservation planning for relict species in the Mediterranean refugia should not be species-independent, but taxon specific.

Conclusions

On the whole, it could be reported that fine-scale spatial patterns of Z. abelicea indicate that processes related to the persistence of the species-to-climate changes are more complicated and multifactorial than a linear and plain view of survival in climate refugial areas.

Zelkova abelicea tolerates disturbance or track changes resulting from disturbance in the range of its distribution through morphological and reproductive plasticity, so its persistence was not only a matter of isolated enclaves in suitable climate space. Indications of plant–plant interactions, such as the assumed mutualistic relationship, further support this view, also classifying Z. abelicea as a BS species, which requires for its persistence a mutualist that is also limited by climate.

Therefore, incorporation of the aforementioned points in future conservation planning seems to be of essential priority, and we call for a shift in the attention of conservation practitioners from spatial patterns to processes which are related to the persistence of the species to climate change.

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