EFFECT OF CLIMATE CHANGE ON FIR FOREST COMMUNITIES IN THE MOUNTAINS OF SOUTH-CENTRAL GREECE

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ABSTRACT

The endemic oro-Mediterranean fir (*Abies* spp.) forests in Greece are valuable ecosystems with high ecological and economic importance. In the mountains in south-central Greece, the availability of moisture plays a crucial role in the floristic composition, structure and distribution of fir forest communities. Because of the predicted adverse climate changes for the Mediterranean zone, suitability of many habitats for the growth of fir forests will change. This study aims to quantify the degree to which these forests will be affected by climate change. Current and future climatic conditions in the area studied were estimated for two periods of time (2041 – 60, 2061 – 80) and two climate change scenarios (RCP 4.5, RCP 8.5). Vegetation relevés were classified and ordinated. Recursive partitioning was used to reveal the most important factor for discriminating the main plant communities and determining the ecological threshold between them. Current and future suitability of bioclimatic space for fir forest communities was identified. The effect of climate change was assessed based on predicted changes in the potential distribution, in terms of size and location, of fir forest communities. Two plant communities that reflect the differentiation of fir forests into xerophytic and mesophytic forest types are described. Among several climatic variables, spring drought was the best factor discriminating these two forest communities. The quantification of the threshold for drought in these two plant communities was used to predict their potential distribution in the area studied. Potential distribution of fir forests in south-central Greece will change in the future, due to a reduction in suitable bioclimatic space and shift to higher altitudes. The effect is expected to be greater for xerophytic forest communities, especially in the worst-case scenario (RCP 8.5) and in 2061–80.

Keywords: *Abies cephalonica*; *Abies* x *borisii-regis*; exposure; MaxEnt; sensitivity; Sterea Ellas

Introduction

Fir (*Abies* spp.) forests are a widespread landscape feature in the mountains of southern and central Greece, with high ecological and economic importance. Three closely related fir taxa occur in Greece, *Abies cephalonica* Loudon (Greek fir), *A. alba* Mill. (silver fir) and their natural hybrid *A.* × *borisii-regis* Mattf. (Mitsopoulos and Panetsos 1987; Christensen 1997). The endemic Greek fir is the dominant forest species in the mountains of Peloponnese (southern Greece) and Sterea Ellas (south-central Greece). In the northern mainland part of Greece, Greek fir is replaced by *A.* × *borisii-regis*. The silver fir is only found in the northernmost parts of the mainland (Christensen 1997).

Although fir forests in Greece receive abundant precipitation during autumn and winter, they may suffer from drought in summer (Aussenac 2002). Drought plays a crucial role in the floristic composition, structure and distribution of coniferous forest communities in southern and south-central Greece (Bergmeier 2002; Samaras et al. 2015). In south-central Greece, there are two types of fir forest vegetation: mesophytic and xerophytic (Samaras et al. 2015). Drought is the main abiotic factor that affects and weakens fir trees, making them vulnerable to bark beetle attacks (Tsopelas et al. 2004). Periods of extreme drought can cause extensive dieback as occurred in 1988–89 throughout Greece, and more recently in 2000–02 and 2009 on many mountains in southern and central Greece (Markalas 1992; Brofas and Economidou 1994; Raftoyannis et al. 2008).

Climate change projections for the Mediterranean zone indicate that extremely dry years will occur more frequently and drought periods will be much longer in the future (Lindner et al. 2014). Because of these environmental changes, dieback and mortality of fir forests may increase in the future. Climate change will also affect the suitability of many habitats for the growth of fir forests, which are expected to result in a change in their distribution associated with the new conditions. Vegetation dynamic models indicate a possible shift of fir forests to higher altitudes (Fyllas and Troumbis 2009; Fyllas et al. 2017). Species distribution models are another useful tool, which are extensively used to analyse the effect of climate change on different species (Elith and Leathwick 2009; Navarro-Cerrillo et al. 2018).

For the protection, conservation and rational utilization of the valuable fir forest ecosystems in Greece, it is necessary to take appropriate management measures, which will help to address the effect of climate change (Chrysopolitou and Dafis 2014). However, in order to adapt forest management to climate change, the most affected areas must be identified and the degree to which fir forests might be affected by climate change determined.

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We hypothesize that:

1. potential distribution of fir forests in Greece will shift to higher altitudes;
2. climate change will mostly affect xerophytic fir forest communities

To test these hypotheses, we chose a representative area in south-central Greece covered by extensive fir forests, to analyse and quantify the degree to which these forests will be affected by climate change. Our *objectives* were:

- to estimate current and future climatic conditions in the area studied;
- to study the floristic and ecological differentiation of fir forests in the area studied;
- to identify current and future suitability of bioclimatic space for fir forests;
- to assess the effect of climate change on fir forest plant communities in the area studied.

Material and methods

Study area

The area studied is located in the central part of south-central Greece (Sterea Ellas). The area consists of three mountains (Goulinas, Vardousia and Iti), rising to 2495 m a.s.l. (summit of Korakas) and lies between 38°32´30″ and 38°56´42″ N and 21°57´24″ and 22°29´30″ E (Fig. 1).

The dominant type of forest in this region is the endemic oro-Mediterranean *Abies cephalonica* or mixed *A. cephalonica* and *A.* × *borisii-regis* forest, which covers 29% of the area studied. *A.* × *borisii-regis* is considered a natural hybrid between *A. alba* and *A. cephalonica* and is morphologically intermediate between these two species (Christensen 1997). Recent studies on the genetic variation of fir populations in Greece have confirmed that *A.* × *borisii-regis* cannot be distinguished from *A. cephalonica* based on isozyme or molecular markers (Fady and Conkle 1993; Scaltsoyiannes et al. 1999; Drouzas 2000) and it is often difficult to distinguish them based on morphological traits. For the purposes of this study all fir trees in the area studied are considered to belong to the species *A. cephalonica* s.l.

The dominant bedrock in the area studied is flysch, while Jurassic limestone and scree slopes (or terraces) occur to a small extent (Kallergis et al. 1970). The climate in the fir forest zone is typically Mediterranean with wet, cool winters and dry summers. Nevertheless, there are large local differences due to the complexity and variety of the topography.

Climatic analysis

The knowledge of current and future climatic/bioclimatic conditions is an important element in any assessment of the effect of climate change. We, therefore, estimated the *current local climatic conditions* in the area studied and generated high-resolution climatic maps

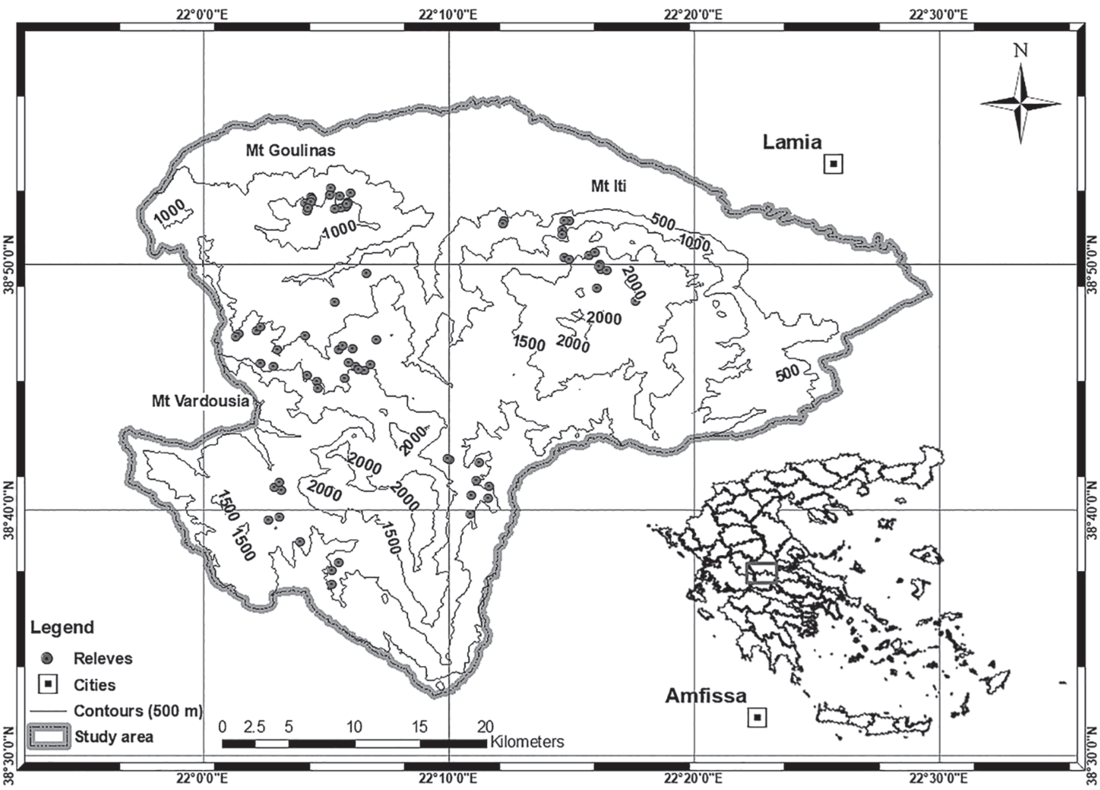

Fig. 1 Map of the are studied with the location of the 67 plots indicated by black dots. Coordinate reference system: WGS 84.

(horizontal resolution of 3 arc seconds ~ 90 m). The raster maps were generated for different time periods such as monthly periods, the driest period (4 driest months, June–September), vegetation period (April to October), annual period and four seasons.

For the spatial estimations of *air temperature* (T) and *precipitation* (P), we used ordinary kriging, linear regression and regression-kriging models. In the estimate, we accounted for altitude and the spatial correlation of the climatic data from 20 weather stations over the period 1975–2010 (Samaras et al. 2017). The computational steps follow the general framework for geostatistical mapping of environmental variables in Hengl (2009). To calculate the monthly mean of daily *global irradiation* (Rs), the r.sun model (Hofierka and Šúri 2002; Šúri and Hofierka 2004) was used in the GRASS-GIS software version 7.2 (GRASS Development Team 2017). The model considers the spatial variation of fine-scale physiographic features like altitude, surface inclination, exposure and topographic shadowing effects. For the analytical computational steps see Samaras et al. (2017). The *reference potential evapotranspiration* (PETref) was calculated by using the empirical equation of Abtew (1996), for which maximum air temperature (Tmax) and Rs values, calibrated for the local conditions, are required (Samaras et al. 2014). For the quantification of drought, we used a modified version of the Transeau's *Humidity Index* (HI – Tuhkanen 1980), which combines the two main factors related to drought. The HI was calculated as the ratio of P to PETref (HI = P/PETref). Nineteen bioclimatic variables were created from monthly data of P, Tmax and Tmin, using "dismo" R package (Hijmans et al. 2021).

For the estimation of the *future local climatic conditions*, we used the CHELSA-[CMIP5] climatic dataset for the years 2041–2060 and 2061–2080 (https://chelsa-climate.org/future/). CHELSA-[CMIP5] climatic data are based on the 1979–2013 reference CHELSA climatic dataset (Karger et al. 2017) and consist of temperature and precipitation estimates at a horizontal resolution of 30 arc seconds (1 km) in the form of raster (GeoTIFF) files. In order to take into account the uncertainty of future climates, due to different future anthropogenic greenhouse gas emissions, we used 2 different scenarios (RCP 4.5 and RCP 8.5), proposed by the IPCCs fifth assessment report (IPCC 2013). The RCP 4.5 scenario is nearly equivalent to Paris accord emission reduction, while the RCP 8.5 represent current rates of emissions (Schwalm et al. 2020). From the 36 Earth system models of the CMIP5 ensemble, we chose 5 models (CESM1-CAM5, FIO-ESM, GISS-E2-H, IPSL-CM5A-MR, MIROC5) that show the lowest amount of interdependence, according to Sanderson et al. (2015). By averaging the projected climatic conditions of the 5 models, we obtained estimates of the future temperature and precipitation for the area studied (future CHELSA climatic data). In order to further downscale the future CHELSA climatic data at a higher horizontal resolution (3 arc seconds), we calculated temperature and precipitation changes as percentage of reference CHELSA climatic data. Then we added or extracted these changes from the raster maps of the current climatic conditions, generating the future temperature and precipitation estimates for the area studied at a horizontal resolution of 3 arc seconds (future climatic data). To simplify the calculation, we assumed that there will be no changes in the monthly mean daily global irradiation in the future. The future climatic data for temperature (means, max, min) and precipitation were finally used to estimate future possible changes in PETref and HI for different time periods and 19 more bioclimatic variables.

Vegetation analysis

The aim of the vegetation analysis was to study the floristic and ecological differences of the mesophytic and xerophytic fir forest plant communities, to delineate their distributions and, finally, predict their current distribution in the area studied.

For the vegetation analysis, 50 personal, unpublished relevés from the current distribution range of fir forests in the area studied were selected. At each location, a rectangular plot of 200 m^2 was sampled. In each plot, the species composition was recorded. Structural information was obtained by assessing the covers of three layers of vegetation (herb, shrub and tree layer). For all species and layers, the cover-abundance was estimated using the extended (9-point) Braun-Blanquet scale (Van der Maarel 2006). The nomenclature of vascular plants follows Dimopoulos et al. (2013, 2016). Topographic information was recorded for each plot including altitude, inclination and exposure. Exposure (measured in degrees) is considered to be a poor variable for quantitative analysis (McCune and Keon 2002) and therefore has to be transformed prior to data analysis. Two new variables were created, "exposure to the north" and "exposure to the east", with the use of trigonometric functions (Leyer and Wesche 2007). Additional vegetation data from 17 relevés were obtained from Samaras et al. (2008, 2015).

Vegetation relevés were classified based on the floristic composition and species cover values. A hierarchical agglomerative *cluster analysis* based on Bray-Curtis distance (Bray and Curtis 1957) was performed. For the determination of diagnostic taxa for the vegetation units, fidelity values for the species were calculated using a modification of the Φ index (Tichý and Chytrý 2006). To reveal expected gradients in vegetation, *Non-Metric Multidimensional Scaling* (NMDS) was used (Kruskal 1964a,b), with Bray-Curtis distance. *Recursive partitioning* was used to derive classification trees for the response variables (plant communities) (Breiman et al. 1984), in order to reveal the most important factor for the discrimination of the main plant communities and to determine the threshold between them. All the analyses wer performed in R software, version 4.0.3 (R Core Team 2020), with the use of various R packages. The computational

Table 1 Sensitivity effect categories based on the threshold values of overlap and ratio metrics.

	Overlap and Ratio Sensitivity thresholds (%)							
	< 30	30–50	50–70	70–100	100–130	130–150	150–170	> 170
Overlap effect category	Very High	High	Moderate	Low				
Ratio effect category	Very High	High	Moderate	Low	Low	Moderate	High	Very High
	Negative Effect				Positive Effect			

steps follow the general framework of the data analysis in Samaras et al. (2015).

Assessment of the effect of climate change

Effect is a function of *exposure* and *sensitivity* to climate change, without considering the adaptive capacity of a species. *Exposure* is the nature, magnitude and rate of climatic change experienced by a species (external factor) (IPCC 2007). *Sensitivity* is the degree to which a species is affected by climate change (intrinsic factor) (IPCC 2007, 2013).

The methodology used to assess the effect of climate change on fir forest plant communities is based on a modification of the analytical framework of Sajwaj et al. (2009) and Harley et al. (2010). As a measure of exposure to climate change, we used the *projected future climatic conditions* for the area studied. Sensitivity assessment was based on changes in the *potential distribution* (in terms of size and location) of *Abies cephalonica* s.l. in terms of two metrics:

1. *Overlap* – the percentage of *current potential distribution* (current suitable bioclimatic space) that is covered by the *projected future potential distribution* (future suitable bioclimatic space).
2. *Ratio* – the relative change in total potential distribution range (suitable bioclimatic space).

Overlap and ratio metrics were used to define *effect categories* based on the threshold values of Table 1 (from Sajwaj et al. 2009). Overlap indicates the need for shifting species range in order to maintain the total area of its current distribution. Ratio indicates a reduction or expansion of total suitable bioclimatic space.

To estimate the *future potential distribution* of *Abies cephalonica* s.l., we used a species distribution modeling (SDM) analysis (MaxEnt). MaxEnt (Phillips et al. 2006; Pearson et al. 2007; Phillips and Dudík 2008) is a machine learning niche model that describes the correlation between a focal species current distribution (using presence-only data) and a set of environmental variables. The SDM analysis was done using the MaxEnt software version 3.4.1 (Phillips et al. 2021). The geospatial analysis was implemented in QGIS (QGIS Development Team 2021).

The *current actual distribution* of fir forests was obtained from vegetation maps of the area studied. The maps were digitized at the same resolution with climatic data (3 arc seconds). From the current actual distribution of fir forests, we randomly selected 20% of all grid cells, which corresponds to 11,648 occurrences of *Abies cephalonica* s.l. We repeated this procedure 10 times, creating 10 distribution datasets. Initially, 29 environmental variables were selected as predictors. Among them, PETref and HI for the 4 driest months, vegetation period, spring, summer and autumn and 19 more bioclimatic variables. In order to avoid multicollinearity among the continuous climatic variables, we calculated Pearson correlation coefficients between all possible combinations of variables. All variables with high correlations (r > |0.75|) were excluded from the analysis.

For each fir distribution dataset, we ran 10 models with MaxEnt using the default settings and the auto-features mode, as suggested by Phillips and Dudik (2008). Seventy five percent (75%) of fir species' occurrences were used to train MaxEnt models while the remaining 25% was used to test the accuracy of each model. The output of the model (a continuous suitability map) was converted into presence/absence data by using the Equal Training Specificity and Sensitivity threshold. The effect assessment procedure was carried out for both fir species and their plant communities.

Results

Current and future climatic conditions

Several thematic maps were created showing the current and future climatic conditions in the area studied

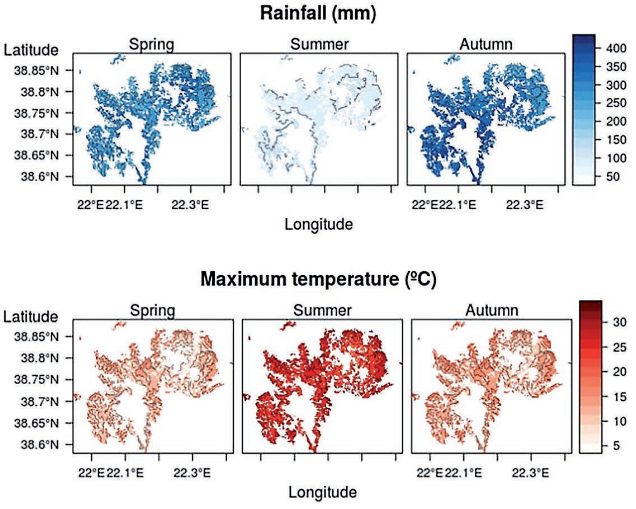

Fig. 2 Mean seasonal values of rainfall and average maximum temperature in the current distribution of fir forests in the area studied.

Table 2 Range of the predicted seasonal values for Humidity Index (HI) for two periods of time (2041–60, 2061–80) and two climate change scenarios (RCP 4.5, RCP 8.5). The HI values for the reference period (1979 to 2013) are in bold and the largest changes are underlined.

Time	Scenario	Spring	Summer	Autumn	Vegetation period
1979–2013		**0.42–4.27**	**0.07–0.38**	**0.66–6.39**	**0.17–1.19**
2041–2060	RCP 4.5	0.37–3.36	0.07–0.35	0.60–5.59	0.15–1.04
2041–2060	RCP 8.5	0.33–2.96	0.06–0.31	0.53–5.14	0.12–0.91
2061–2080	RCP 4.5	0.34–3.13	0.06–0.32	0.60–5.62	0.14–0.99
2061–2080	RCP 8.5	0.30–2.59	0.05–0.28	0.47–4.51	0.11–0.81

(Fig. 2). In the current distribution area of fir forests, mean seasonal rainfall varies between 145 to 355 mm during spring, 50 to 130 mm during summer and between 162 to 414 mm in autumn (Fig. 2). The average maximum temperature ranges between 5.3 and 21.1 °C in spring, 18.1 and 32.5 °C in summer and between 7.2 and 23.0 °C in autumn (Fig. 2). Global irradiation during vegetation period ranges from 7.6 to 22.7 Mj/m^2. PETref during vegetation period varies between 341 and 1119 mm and HI, for the same period, ranges from 0.17 to 1.19 (Fig. 3).

Based on both RCP greenhouse gas emissions scenarios (RCP 4.5 and RCP 8.5), HI index is predicted to gradually decline up to 2080. The largest decrease in HI is expected during spring and autumn, while smaller changes are expected during summer (Table 2).

Plant communities

The classification of the vegetation plots revealed two plant communities (Table 3), clearly distinguishable by their floristic and ecological characteristics. The two plant communities are:

Plant community A (Xerophytic forest) (Table 3, A): this community is made up of pure fir forest stands and mixed stands of *Abies cephalonica* s.l. with *Quercus petraea* subsp. *polycarpa* and occasionally *Q. frainetto* or *Q. pubescens*. The shrub layer consists mainly of *Abies cephalonica* s.l., *Juniperus oxycedrus* subsp. *oxycedrus* and *Quercus coccifera*. Many other woody species such as *Quercus frainetto*, *Fraxinus ornus*, *Ilex aquifolium* and *Phillyrea latifolia* occur at a lower frequencies in the shrub layer. It is characterized by a group of thermophilous plants indicative of dry conditions (i.e. *Quercus coccifera, Sedum cepaea, Fraxinus ornus, Cistus creticus, Asplenium onopteris*).

Plant community B (Mesophytic forest) (Table 3, B): this community is made up of pure fir forest stands and mixed stands of *Abies cephalonica* s.l. with *Fagus sylvatica* subsp. *sylvatica*. The shrub layer consists mainly of *Abies cephalonica* s.l., and *Juniperus oxycedrus* subsp. *oxycedrus.* A few other woody species (i.e. *Juniperus communis* subsp. *nana* and *Sorbus aria*) occur at low frequencies in the shrub layer. It is differentiated from the xerophytic community by a group of species indicating moderately moist conditions (i.e. *Geum urbanum*, *Arabis alpina*, *Bromus benekenii*).

Multivariate analysis of floristic data identified the main vegetation gradient, depicted by the horizontal axis (NMDS1) of the ordination diagram (Fig. 4). The two plant communities were well differentiated along the gradient, with the xerophytic community occupying the left part of the ordination diagram and the mesophytic community the right part (Fig. 4). By fitting different environmental variables onto the ordination scores, the underlying ecological gradient that explains the floristic differentiation of the fir forests was revealed. The direction and strength of the ecological gradients is represented by the direction and length of the vectors respectively (Fig. 4). The horizontal axis of the ordination diagram reflects a seasonal drought gradient that was quantified using the HI index. The left part of the ordination diagram represents areas of low altitude and humidity, while the right part more humid areas of high-altitude fir forests.

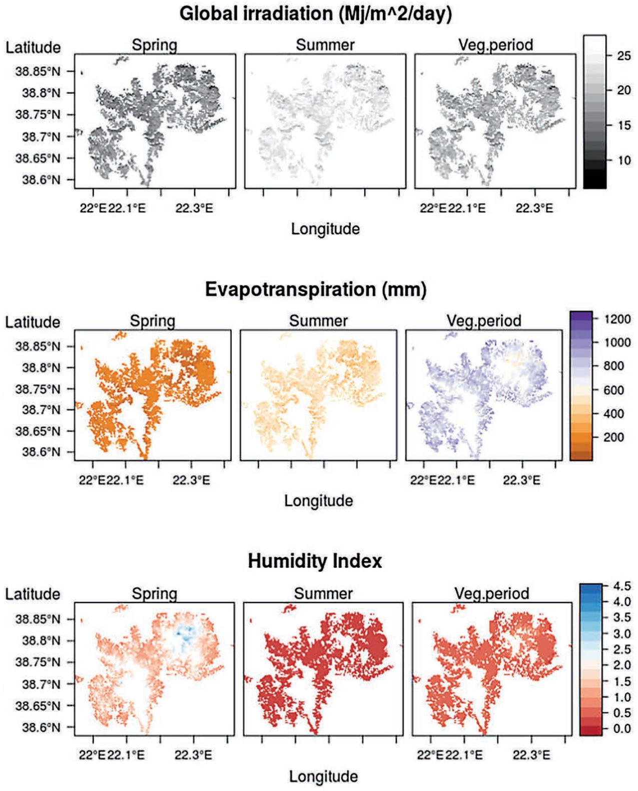

Fig. 3 Global irradiation, potential evapotranspiration and Humidity Index in spring, summer and vegetation period (April to October) in the current distribution of fir forests in the area studied.

Table 3 Synoptic table of the fir forest vegetation units (plant communities) in the area studied based on cluster analysis (Flexible beta with β = −0.25, Bray-Curtis distance). Only the diagnostic taxa are presented along with their frequency (Freq), fidelity (Φ) and indicator (IndVal) values.

Communities	**A (n = 44)**	**B (n = 23)**			
Number of relevés (n = 67)	**Freq (%)**	**Freq (%)**	**Φ**	**IndVal A**	**IndVal B**
Community A (Xerophytic forest)					
Luzula forsteri subsp. *rhizomata*	89	17	0.714	0.869	0.886
Quercus coccifera	66	4	0.645	0.982	0.659
Crepis fraasii subsp. *fraasii*	64	4	0.626	0.919	0.636
Sedum cepaea	50	0	0.577	1.000	0.500
Carex distachya	45	0	0.542	1.000	0.455
Fraxinus ornus	43	0	0.525	1.000	0.432
Cistus creticus	34	0	0.453	1.000	0.341
Torilis arvensis	34	0	0.453	1.000	0.341
Pilosella bauhini subsp. *magyarica*	52	13	0.418	0.819	0.523
Trifolium grandiflorum	39	4	0.417	0.932	0.386
Quercus petraea subsp. *polycarpa*	30	0	0.416	1.000	0.296
Thymus longicaulis	36	4	0.398	0.954	0.364
Asplenium adiantum-nigrum	27	0	0.397	1.000	0.273
Asplenium onopteris	25	0	0.378	1.000	0.250
Hedera helix subsp. *helix*	25	0	0.378	1.000	0.250
Digitalis laevigata subsp. *graeca*	23	0	0.358	1.000	0.227
Prunella vulgaris	23	0	0.358	1.000	0.227
Ruscus aculeatus	23	0	0.358	1.000	0.227
Community B (Mesophytic forest)					
Lapsana communis subsp. *adenophora*	20	96	0.762	0.833	0.957
Pilosella cymosa subsp. *sabina*	5	70	0.673	0.949	0.696
Lamium garganicum subsp. *garganicum*	5	65	0.637	0.943	0.652
Stellaria media	16	78	0.625	0.884	0.783
Sedum hispanicum	9	65	0.581	0.907	0.652
Geum urbanum	11	61	0.515	0.897	0.609
Silene multicaulis subsp. *multicaulis*	9	57	0.505	0.940	0.565
Arabis alpina	7	52	0.497	0.950	0.522
Digitalis ferruginea subsp. *ferruginea*	7	52	0.497	0.909	0.522
Dactylis glomerata	45	91	0.493	0.733	0.913
Geocaryum capillifolium	32	78	0.467	0.796	0.783
Festuca rubra subsp. *juncea*	0	35	0.459	1.000	0.348
Verbascum epixanthinum	0	35	0.459	1.000	0.348
Myosotis sylvatica subsp. *cyanea*	66	100	0.453	–	–
Arrhenatherum elatius	25	70	0.446	0.822	0.696
Carduus tmoleus subsp. *cronius*	0	30	0.424	1.000	0.304
Ranunculus sartorianus	0	30	0.424	1.000	0.304
Pimpinella tragium subsp. *polyclada*	2	35	0.418	0.976	0.348
Galium aparine	11	48	0.399	0.902	0.478
Aremonia agrimonoides	73	100	0.397	–	–
Daphne oleoides subsp. *oleoides*	0	26	0.387	1.000	0.2609
Bromus benekenii	2	30	0.381	0.976	0.3043
Cardamine hirsuta	20	57	0.371	0.761	0.5652
Acinos alpinus	11	43	0.360	0.779	0.4348
Silene vulgaris	11	43	0.360	0.877	0.4348

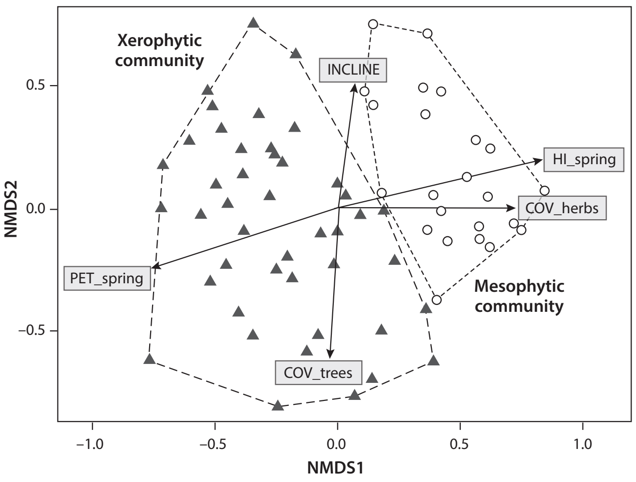

Fig. 4 Distribution of the vegetation units along the two axes (NMDS1, NMDS2) of the ordination (NMDS). The different symbols indicate vegetation units identified by the cluster analysis. The envelopes include the two main plant communities. The stress for the solution with two axes is equal to 0.18. Three environmental variables are projected as vectors on the ordination. The direction and strength of the gradients is represented, respectively, by the direction and length of the vectors.

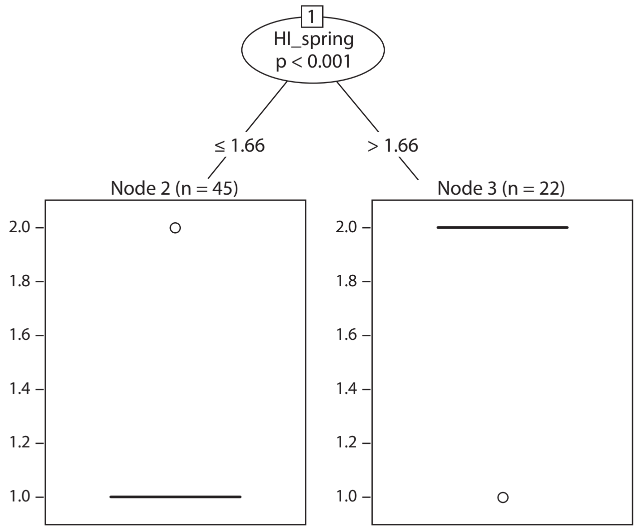

Fig. 5 Classification tree for the two fir forest communities (Node 2 = Xerophytic community; Node 3 = Mesophytic community) based on environmental variables. The drought threshold is indicated by HI_spring (Humidity Index during spring). The level of significance chosen was α = 0.05.

Recursive partitioning revealed HI during spring (HI_spring) as the best discriminating variable among all the factors analysed (Fig. 5). Most of the plots from the xerophytic forest community were included in the left panel of the classification tree (Fig. 5, Node 2), while the majority of the plots from the mesophytic forest community were included in the right panel (Fig. 5, Node 3). A xerophytic forest community is present when the value of HI in spring is less or equal to 1.66. In contrast, the occurrence of the mesophytic forest community is associated with HI_spring values of more than 1.66. No other plot subgrouping was detected using any of the remaining environmental variables analysed in this study. The above ecological threshold value was used to predict the

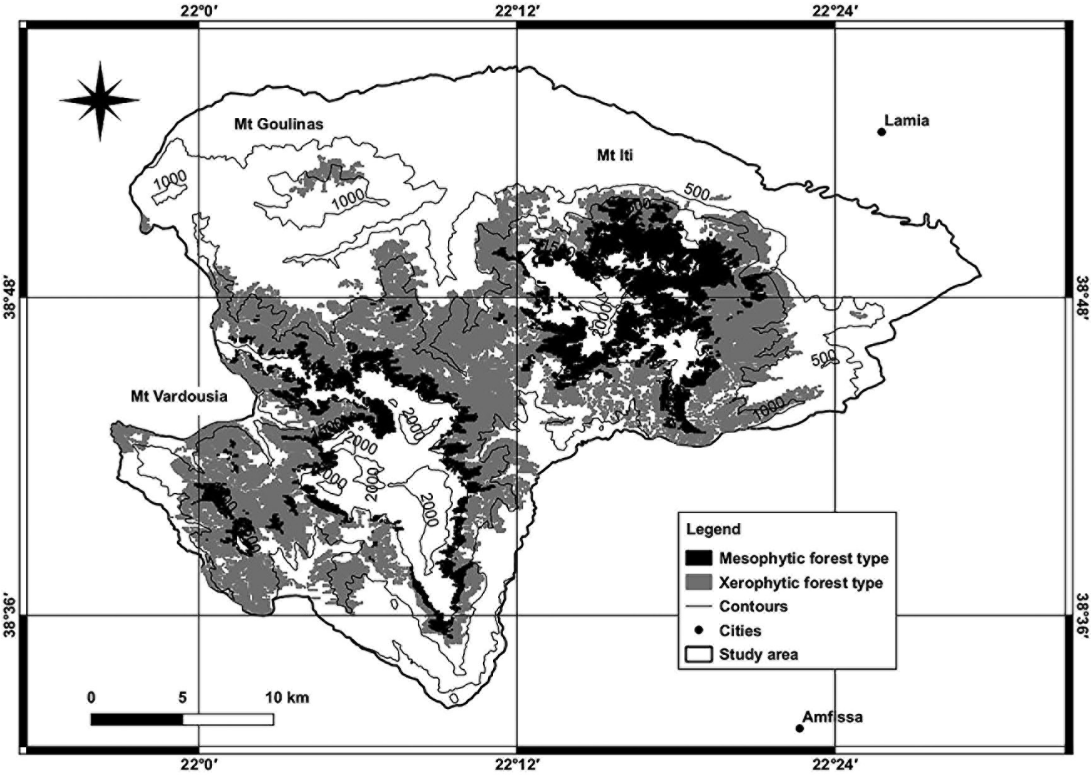

Fig. 6 Map of the area studied with the current actual distribution of Xerophytic (grey colour) and Mesophytic (black colour) fir forest stands. The distribution threshold of the two fir forest communities is based on their ecological threshold of HI_spring (Humidity Index during spring).

Table 4 Heuristic estimate of relative contributions of the variables (%) included in the analysis (bio1: annual mean temperature, bio8: mean temperature in wettest quarter, bio12: annual precipitation, HI_spring: Humidity Index in spring, PET_dry: Potential Evapotranspiration in the 4 driest months – June to September).

MaxEnt model	bio1	bio8	bio12	HI_spring	PET_dry
Model 1	3.2	3.0	1.7	83.5	8.6
Model 2	2.9	3.0	1.7	86.1	6.4
Model 3	3.5	2.9	1.6	83.3	8.7
Model 4	2.9	2.9	2.0	83.8	8.4
Model 5	3.2	3.0	1.7	83.8	8.3
Model 6	3.1	2.6	1.9	83.8	8.6
Model 7	2.4	2.8	2.3	86.5	6.0
Model 8	2.9	2.8	1.7	86.4	6.3
Model 9	3.0	2.7	1.7	86.1	6.6
Model 10	3.4	2.3	1.8	83.7	8.7
Average	**3.1**	**2.8**	**1.8**	**84.7**	**7.7**

current actual distribution of the two plant communities in the area studied (Fig. 6).

Xerophytic communities occur on Mt. Vardousia, Mt. Goulinas and Mt. Iti, in the meso-Mediterranean and the lower part of the supra-Mediterranean zones, between 660 and 1360 m a.s.l. Mesophytic communities occur on Mt. Iti and Mt. Vardousia at higher altitudes (1230–1840 m a.s.l.) than the previous community and is totally absent from Mt. Goulinas. It ranges from the lower part of the supra-Mediterranean zone up to the timberline (Fig. 6).

Suitability of bioclimatic space for fir forests

Of the 29 environmental variables that were selected as predictors, only 5 (HI_spring, PET_dry, bio1, bio8, bio12) had low intercorrelations (r < |0.75|) and therefore were included in the MaxEnt model. The most important variable, defined by the MaxEnt model, was by far

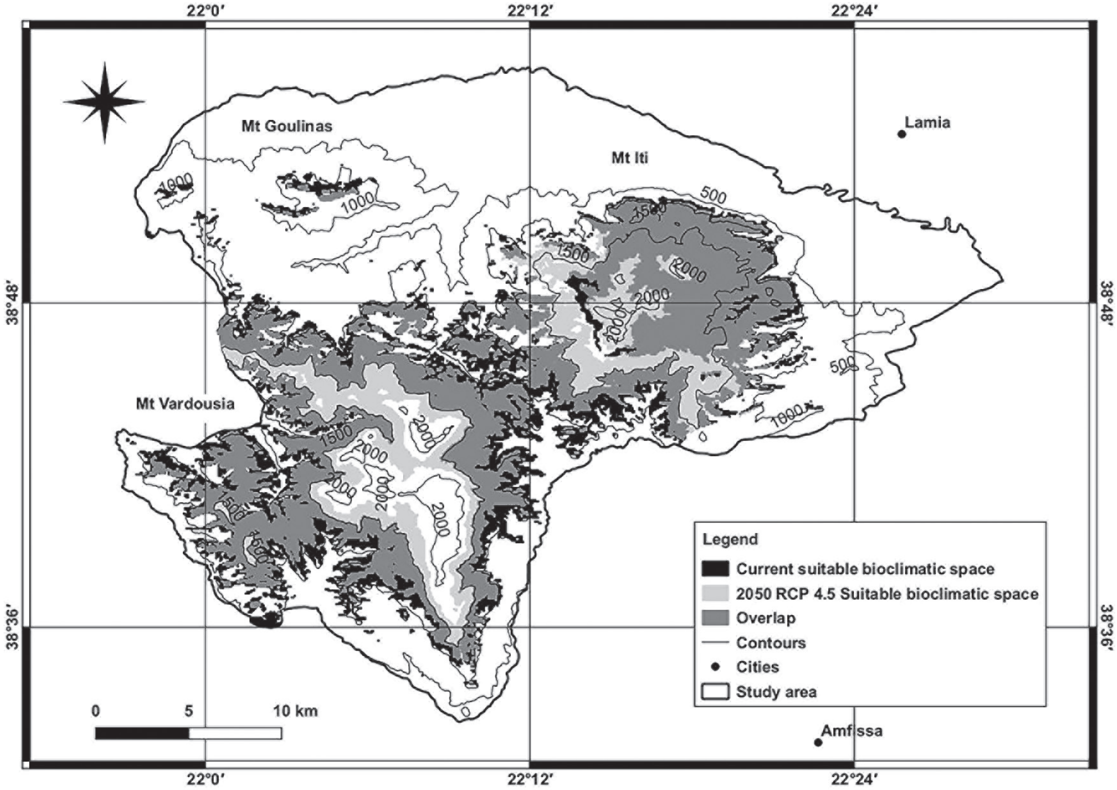

Fig. 7 Map of the area studied with the current suitable bioclimatic space (black colour), the predicted suitable bioclimatic space in 2050 for the RCP 4.5 scenario (light grey colour) and their overlap (dark grey colour).

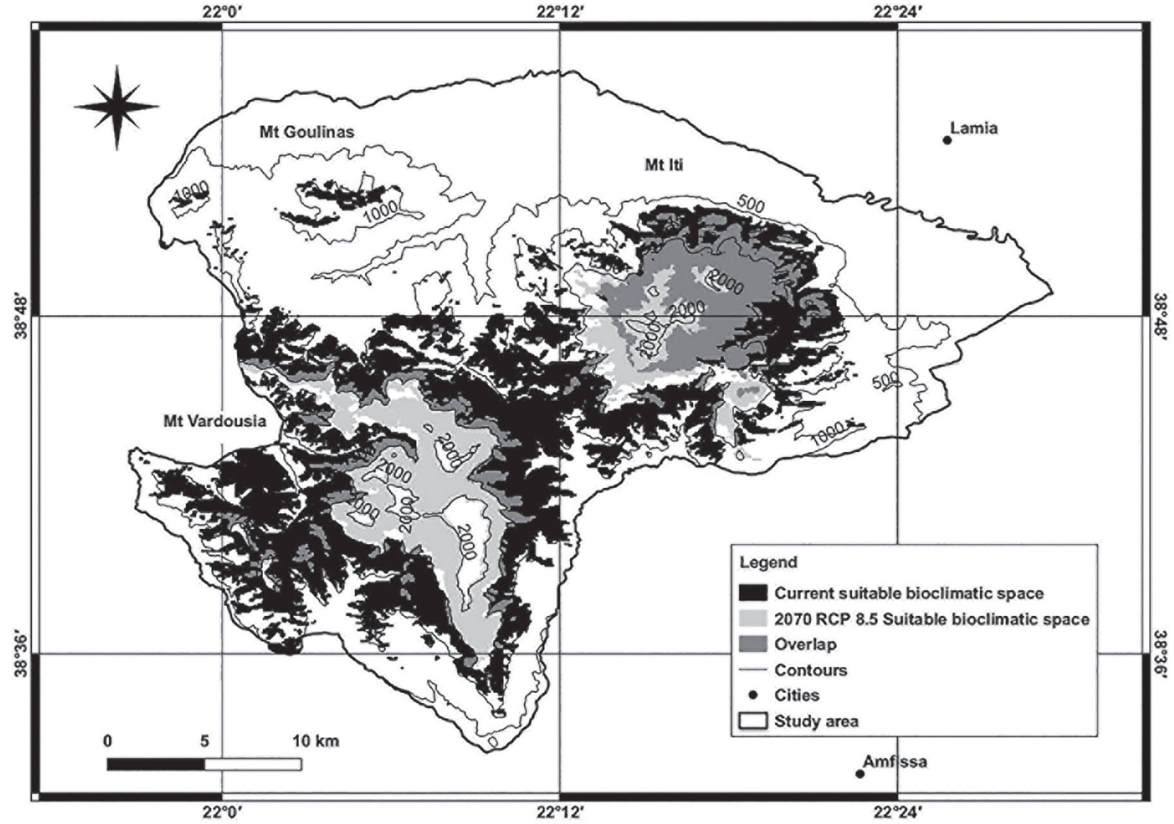

Fig. 8 Map of the area studied with the current suitable bioclimatic space (black colour), the predicted suitable bioclimatic space in 2070 for the RCP 8.5 scenario (light grey colour) and their overlap (dark grey colour).

HI_spring (84.7%) followed by PET_dry (7.7%), while the least important variable was bio12 (1.8%) (Table 4).

The current suitable bioclimatic space for *Abies cephalonica* s.l., predicted by the MaxEnt models, covers an area of 31,515.9 ha. Based on the RCP 4.5 scenario, the future suitable bioclimatic space is predicted to decline to 30,256.3 ha by 2050 (Fig. 7) and to 21,990 by 2070. The suitable bioclimatic space for fir forests is predicted to be even smaller following the RCP 8.5 scenario (22,555.9 ha by 2050 and 16,554.1 by 2070) (Fig. 8).

Effect of climate change

The effect of climate change on fir forests varies and depends on the projected period and the emissions scenario. Considering the whole distribution of fir forests, a moderate to very high effect of overlap and a low to moderate ratio is expected (Table 5).

If we consider the RCP 4.5 scenario, the effect of climate change on fir forests due to the reduction of suitable bioclimatic space (ratio) is expected to be low in 2050 (96%) and moderate in 2070 (69.8%), see Table 5. The negative effect of ratio is expected to be higher for the xerophytic plant community, with a value of 93.5% in 2050 and 66% in 2070 (Table 6). In contrast, the mesophytic community is expected to have a positive effect of ratio in 2050 with an expansion of its suitable bioclimatic space (102.6%) and a low negative ratio in 2070 (79.8%). Based on the RCP 8.5 scenario, although the reduction of suitable bioclimatic space is expected to be higher, compared to the RCP 4.5 scenario, the ratio effect on fir forests is projected to be low in 2050 (71.6%) and moderate in 2070 (52.5%), see Table 5. In 2050 the negative ratio effect is expected to be almost the same for both xerophytic and mesophytic communities, but in 2070 a higher neg-

Table 5 The overlap and ratio metrics for the assessment of the effect of climate change on fir forests in two periods of time (2041 – 60, 2061 – 80) and for two climate change scenarios (RCP 4.5, RCP 8.5).

Time	Scenario	Overlap	Overlap effect	Ratio	Ratio effect
2050	RCP 4.5	65.2%	Moderate	96.0%	Low
2050	RCP 8.5	39.8%	High	71.6%	Low
2070	RCP 4.5	41.7%	High	69.8%	Moderate
2070	RCP 8.5	21.1%	Very high	52.5%	Moderate

Table 6 The overlap and ratio metrics for the assessment of the effect of climate change on fir forest communities in two periods of time (2041 – 60, 2061 – 80) and for two climate change scenarios (RCP 4.5, RCP 8.5).

Time	Scenario	Xerophytic community				Mesophytic community			
		Overlap	Overlap effect	Ratio	Ratio effect	Overlap	Overlap effect	Ratio	Ratio effect
2050	RCP 4.5	53.6%	Moderate	93.5%	Low	42.0%	High	102.6%	+ Low
2050	RCP 8.5	18.7%	Very high	71.5%	Low	27.8%	Very high	71.7%	– Low
2070	RCP 4.5	24.9%	Very high	66.0%	Moderate	30.6%	High	79.8%	– Low
2070	RCP 8.5	1.6%	Very high	48.9%	High	10.6%	Very high	62.2%	– Moderate

ative ratio effect is predicted for xerophytic communities (48.9%), see Table 6.

Considering the RCP 4.5 scenario, the overlap effect on fir forests is expected to be moderate in 2050 (65.2%) and high in 2070 (41.7%), see Table 5. The negative overlap effect is expected to be higher for the xerophytic plant community, with a value of 53.6% (moderate) in 2050 and 24.9% (very high) in 2070 (Table 6). The mesophytic community is expected to have a high negative overlap effect in both 2050 (42%) and 2070 (30.6%). Based on the RCP 8.5 scenario, the overlap effect on fir forests is predicted to be high in 2050 (39.8%) and very high in 2070 (21.1%). Very high overlap effect is predicted for both projection periods for the xerophytic and mesophytic communities, although the overlap values for the xerophytic community are predicted to be 10% more than for the mesophytic community (Table 6).

Discussion

Floristic and ecological differentiation between the fir forests

A difference in the fir forest vegetation in xerophytic and mesophytic plant communities was recorded in the area studied. These results confirm those of previous studies on fir forest vegetation in southern and south-central Greece. Bergmeier (2002) reports the same pattern and suggests that water supply is the crucial factor driving the floristic variation of coniferous forests and woodlands of *Abies cephalonica*, *Pinus nigra* and *Juniperus drupacea* on Mt. Parnon (southern Greece). Similarly, Samaras et al. (2015) report that the floristic variation within the fir forest vegetation on the Oxia-North Vardousia mountain system (south-central Greece) reflects the differences between mesophytic and xerophytic forest communities, associated with the seasonal drought gradient from low to high altitudes.

The xerophytic plant community has many floristic elements in common, including two "character species" (*Trifolium grandiflorum* and *Luzula forsteri*), with the association *Trifolio grandiflori-Abietetum borisii-regis* Barbéro and Quézel 1976, described by Barbéro and Quézel (1976) from the mountains of Oxia and Timfristos and the southern part of Mt. Vardousia. It also resembles the *Crepis fraasii-Abies cephalonica* community, described by Samaras et al. (2015) from Mt. Oxia and the northern part of Mt. Vardousia. The mesophytic plant community has many floristic elements in common with the association *Lilio chalcedonicae-Abietetum cephalonicae* Barbéro and Quézel 1976, described by Barbéro and Quézel (1976) from different mountains in Peloponnisos (southern Greece). It also resembles *Abies cephalonica* community described by Karetsos (2002) from Mt. Iti and *Sanicula europaea-Abies cephalonica* community described by Samaras et al. (2015) from Mt. Oxia and the northern part of Mt. Vardousia. A syntaxonomic review of fir forest vegetation in Greece is needed, for a better understanding of their floristic and ecological differentiation. For a rigorous syntaxonomic discussion of Greek fir forests see Samaras et al. (2015).

Possible changes in the distributions of fir forests

Based on the current climatic conditions in the area studied, fir forests are subject to intense water stress during the summer period (Table 2). According to both climatic scenarios, drought intensity is expected to increase significantly during spring and autumn, while in summer the changes are expected to be less severe. Our results are similar to those of previous studies on Mt. Iti (Samaras et al. 2017), confirming the importance of climatic changes (related to drought) in the reduction of suitable bioclimatic space for fir forests.

Both ratio and overlap sensitivity metrics are important for the assessment of the effect of climate change. A low ratio indicates a reduction in the size of a species' potential distribution. On the other hand, a projected low overlap between current and future potential distributions indicates that the species has to shift its range in order to maintain the total area of its current distribution. Although recent studies indicate that such a shift is possible and has already occurred in some tree species (Boisvert-Marsh et al. 2014; Monleon and Lintz 2015), other studies show that range shift may be limited for many species of trees (Zhu et al. 2012). Obstacles (physiographic barriers, dispersal abilities, low levels of breeding productivity, lack of suitable habitat) other than climate can lead a species not shifting its range (Sajwaj et al. 2009). Low levels of overlap, therefore, may result in a higher negative effect, even if the ratio metric is high.

Our results confirm previous studies on the dynamics of vegetation in fir forests in Greece, that show a possible shift in their range to higher altitudes (Fyllas and Troumbis 2009; Fyllas et al. 2017). The shift is predicted to be stronger in the distant future (2061–80). The overlap between current and predicted suitable bioclimatic space in 2070, based on the worst-case RCP 8.5 scenario, is predicted to differ on the three mountains in the area studied (Fig. 8). The effect of climate change will be very high on Mt. Goulinas, where fir forests are expected to disappear by 2070, due to lack of suitable bioclimatic space.

Conclusions

There are two types of fir forests in south-central Greece: mesophytic and xerophytic. The most suitable variable for quantifying the distribution of these two types of forest is the Humidity Index during spring. The potential distribution of fir forests in south-central Greece is expected to change in the future, due to a reduction in suitable bioclimatic space. Furthermore, their potential distribution will shift to higher altitudes, but only in the highest mountains, such as Mt. Iti and Mt. Vardousia. Climate change will mostly affect xerophytic fir forests, which are predicted to loss more than half of their current potential distribution by 2061–80 and in the worst-case RCP 8.5 scenario.

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