Potential impacts of climate change on the distribution of seven dominant tree species in Greece

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Abstract

Purpose: Climate change is expected to affect species distribution and ecosystem form and function. Forests provide a range of ecosystem services including the regulation of local and global climate and understanding their vulnerability to climate change is important for designing effective adaptation strategies. In this study we simulated the distribution of seven dominant tree species in Greece under current and climate change conditions to explore their potential vulnerability.

Methods: We developed species distribution models (SDMs) for each taxon under current climate conditions, using the maximum entropy algorithm. Our training datasets were based on the European Atlas of Forest Tree Species, which was expanded with our own observations and data from forest stewardship plans. Climate and soil data at a resolution of ~1 km² were used as predictive variables. After fitting the SDMs under current conditions and validating their performance, we used the models to project the potential distribution of each species under RCP45 and RCP85 for the 2060-2080 period. We additionally estimated three spatial indices to infer species vulnerability to climate change.

Results:

The distributions of all study species were adequately simulated under current conditions. Following both climate change scenarios significant reductions in the range of potential distribution of all species were simulated except for the two drought tolerant pines.

Conclusions:

Our findings suggest that climate change might significantly affect the distribution and dynamics of the Greek forest sector with important ecological, economic and social implications, and thus adequate mitigation measures should be implemented.
Introduction

In Europe forests cover around 40% of the land, while in Greece the latest FAO estimates indicate that forest cover more than 30% of the total land area. Forests provide several ecosystem services such as climate regulation, water supply, timber, energy, food and habitat for many species. Particularly due to their ability to regulate local and global climate, though carbon and water cycling, forest ecosystem function under current and global change conditions is of great interest for biodiversity conservation and climate adaptation planning (Canadell and Raupach, 2008).

The response of forests to environmental shifts is usually studied with field-based long-term measurements or with ecological models that simulate the response of species and communities to environmental variation. At the European scale, simulations of future vegetation distribution suggest that at least 1/3 of the land surface area may be covered by different (to current) vegetation by the end of the century (Hickler et al. 2012). In southern Europe shifts in the dominant vegetation type are expected to be even more pronounced and widespread replacement of forest from shrubland are simulated, primarily as effect of drier conditions and interactions with fire (Santini et al. 2014). In Greece, a detailed evaluation of how forest will respond to climate change is only available for a limited number of sites (Fyllas et al. 2007, 2017). These simulations agree with the general trend of elevational shifts of species distribution range and the replacement of drought intolerant from drought tolerant species, with positive interactions with the local fire regime also identified (Fyllas and Troumbis 2009).

Although local simulations from process-based ecosystem models are important to understand the mechanisms of shifts in forest function, regional-scale projections under climatic change scenarios are also useful, as they provide an overview of the expected changes. For that purpose, species distribution models (SDMs), or niche models, have been extensively used to model the potential distribution of both species and ecosystems (Elith and Leathwick 2009). A species niche is traditionally (Hutchinson 1957) defined as the “N-dimensional hypervolume where a species could persist”, and in the case of SDMs the N-dimensions are represented by a suite of environmental predictor variables. By modelling a species niche, SDMs help us to understand which are the crucial environmental variables that control a species distribution and how these variables shape the geographic distribution of a species. In practice SDMs simulate species occurrence (or abundance) as a function of several environmental factors, such as climatic and edaphic variables. After fitting an adequate model, the “function” describing species occurrence is used to simulate species distribution across a range of environmental conditions. SDMs provide a quick and spatially explicit simulation of species niche and this is the reason they have been frequently used to study how forests will respond to climate change (Zimmermann et al. 2013, Noce et al. 2017).

The limitation of SDMs are well documented and include: a) uncertainties in environmental predictors and collinearity between them, b) the in-built assumption that the relationship between species presence/absence and environmental predictors (that is parameterised on historical or current distribution data) will maintain under future conditions and c) the fact that SDMs usually have no mechanistic basis and key plant processes related to vegetation dynamics are not taken into account and d) that they are trained based on the realised (after the effect of competition and dispersal limitation) and not the fundamental (physiological) species niche, i.e. a restricted environmental space. In order to take into account these limitations various methods have been developed and implemented. In this paper, which focuses on the potential shifts in the distribution of seven important tree species in
Greece, we concentrate on dealing with the fourth point. In particular, after examining the European Atlas of Forest Tree Species, we noticed a striking under-representation of presence datapoints for seven key forest tree species in Greece (Abies cephalonica, Pinus halepensis, Pinus brutia, Pinus nigra, Quercus pubescens, Quercus frainetto and Fagus sylvatica s.l.). By excluding this set of environmental conditions, probably representing the drier end of the species climatic hypervolume in Europe, the use of SDMs might be biased towards higher vulnerability of these species to climate change. To deal with that we increased the presence points of the seven species with our own observations and data from forest stewardship plans. Subsequently we used empirical species distribution models, to simulate the current and the future distribution of the study species in Greece. We then used these models to project the potential distribution of the species of interest under two climate change scenarios for the year 2070 and estimated three spatial indices to summarise the potential vulnerability of each species to the expected climatic changes.

**Methods**

Detailed species distribution maps are lacking in Greece. For that reason, we used the European Atlas of Forest Tree Species database (San-Miguel-Ayanz et al. 2016) and extend it with our own observations and data from forest stewardship plans. In particular, we increased the very poor representation of only 117 datapoints to 2556 datapoints for Greece in the European Atlas of Forest Tree Species. We added 209 sites with Abies cephalonica occurrence, 128 sites with Pinus halepensis, 431 sites with Pinus nigra, 391 sites with Quercus frainetto, 150 sites with Quercus pubescens and 417 sites with Fagus sylvatica s.l.

Climate data for both current and future conditions were taken from the CHELSA Project (Karger et al. 2017) with a spatial resolution around 1 km². The climate variables used were: the mean annual temperature ($T_a$), the minimum temperature of the coldest month ($T_{min}$), the annual precipitation ($P_a$), the precipitation of the driest month ($P_{dm}$) and the precipitation of the driest quarter ($P_{dq}$). Climate projections from the Max Planck Institute Earth System Model (MPI-ESM-LR) for two emission scenarios (RCP45 & RCP85) and the 2061-2080 period were used to simulate species future distribution. Edaphic data were taken from the European Soil Data Centre (Panagos et al. 2006). In this analysis we used available water capacity (AWC), cation exchange capacity (CEC) and depth to rock (DR) as the key soil variables expressing water and nutrients availability. The edaphic attributes are given on a categorical scale.

The same modelling technique was applied for each species. We initially divided the species occurrence data points into two groups; one (80% of data points) used for training purposes and another one (20%) for validation. We fitted a maximum entropy model (Phillips et al. 2006) and evaluated its performance using standard methods. Model performance was evaluated with the AUC criterion (Area Under the Curve), which is a measure of separability indicating how much each model can distinguish between classes. AUC ranges between 0 and 1 and higher values indicate a better model performance. The optimum SDM of each species was subsequently used to project species distribution across Greece, under current and future climate conditions. We estimated three spatial metrics to evaluate the degree of species range shifts under future conditions. The first metric was estimated as the ratio of future to current area of species potential distribution and indicates the degree of “habitat availability” i.e. whether the areas with favourable condition increase (>1) or decrease (<1) under future conditions. The second metric was defined as the ratio of the future distribution area that overlaps with the current distribution area. This “common area” metric indicates the degree of shrinkage of the current
favourable areas under global warming. The higher the value the smaller the reduction. The third metric is the difference in median elevation between the current and future potential species distribution. The larger the difference the higher the distance populations of the species need to travel to achieve favourable conditions. Dispersal limitations due to anthropogenic activities such as barriers or land use changes were not considered. All analyses and maps were made with the R programming language (R Core Team 2019) and the dismo and rJava packages.

Results

Under current conditions the models simulated adequately the distribution of all species, with an AUC higher than 0.90 in all cases. Table 1 summarises the stronger predictors of species distribution for each of the study species. $T_{\text{min}}$ was a strong predictor for all pine species and Q. pubescens. Dry quarter precipitation strongly contributed to the distribution of A. cephalonica while the precipitation of the driest month was related to the distribution of F. sylvatica. Soil water holding capacity strongly contributed to the distribution of P. nigra and Q. pubescens, while depth to rock was the second strongest predictor of the fir’s distribution.

Table 1: Summary of the maximum entropy models for the distribution of study species. The relative contribution of each environmental variable to the maximum entropy models of the species is also presented, with $T_a$: mean annual temperature (°C), $T_{\text{min}}$: annual minimum temperature (°C), $P_a$: total annual precipitation (mm), $P_{\text{dm}}$: precipitation of the driest month (mm), $P_{\text{aq}}$: precipitation of the driest quarter (mm), AWC: available water holding capacity, CEC: cation exchange capacity, DR: depth to rock.

<table>
<thead>
<tr>
<th>Environmental Variables</th>
<th>Pinus halepensis &amp; Pinus brutia</th>
<th>Pinus nigra</th>
<th>Abies cephalonica</th>
<th>Quercus pubescens</th>
<th>Quercus frainetto</th>
<th>Fagus sylvatica</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_a$</td>
<td>54.3</td>
<td>9.7</td>
<td>9.0</td>
<td>8.2</td>
<td>47.4</td>
<td>14.1</td>
</tr>
<tr>
<td>$T_{\text{min}}$</td>
<td>30.2</td>
<td>49.1</td>
<td>7.0</td>
<td>52.9</td>
<td>8.0</td>
<td>23.3</td>
</tr>
<tr>
<td>$P_a$</td>
<td>0.7</td>
<td>0.4</td>
<td>2.0</td>
<td>9.6</td>
<td>7.7</td>
<td>7.2</td>
</tr>
<tr>
<td>$P_{\text{dm}}$</td>
<td>8.0</td>
<td>2.5</td>
<td>14.3</td>
<td>0.6</td>
<td>9.2</td>
<td>34.1</td>
</tr>
<tr>
<td>$P_{\text{aq}}$</td>
<td>0.7</td>
<td>0.1</td>
<td>33.2</td>
<td>3.2</td>
<td>9.0</td>
<td>0.0</td>
</tr>
<tr>
<td>AWC</td>
<td>5.4</td>
<td>25.6</td>
<td>4.2</td>
<td>17.8</td>
<td>12.2</td>
<td>13.3</td>
</tr>
<tr>
<td>CEC</td>
<td>0.0</td>
<td>1.5</td>
<td>5.3</td>
<td>0.4</td>
<td>2.7</td>
<td>6.4</td>
</tr>
<tr>
<td>DR</td>
<td>0.7</td>
<td>11.0</td>
<td>25.0</td>
<td>7.4</td>
<td>3.7</td>
<td>1.5</td>
</tr>
<tr>
<td>Model performance AUC</td>
<td>0.97</td>
<td>0.92</td>
<td>0.99</td>
<td>0.95</td>
<td>0.96</td>
<td>0.89</td>
</tr>
</tbody>
</table>

When applied under future climate, significant decrease of areas with favourable conditions were simulated for all species apart from the two low-elevation pines, i.e. Pinus halepensis & Pinus brutia (Table 2). Under the RCP45 scenario, by 2070 the total area with favourable conditions is more or less constant (0.95) with 96% of the current potential distribution area remaining within the future geographical space. An increase of 3 m in the median elevation of P. halepensis & P. brutia was projected under RCP45. These shifts were stronger under the RCP85 scenario with an 11% expansion of the potential distribution area and a projected 79 m shift in elevation. On the other hand, a strong
decrease of approximately 79% and 84% of the potential distribution area of *P. nigra* was simulated for RCP45 and RCP85 respectively (associated with an 86 and 367 m shift). The endemic *A. cephalonica* fir is projected to essentially vanish under both climate change scenarios, with its future area of potential distribution shrinking to 5 and 2% of the current under RCP45 and RCP85 respectively.

The projected total area of *Q. pubescens* potential distribution decreased around to half compared with current conditions for both climate change scenarios (58% and 50% for RCP45 and RCP85 respectively), with an associated elevation shift of 33 and 231 m (Table 2). *Q. frainetto* is projected to experience a decrease in habitat availability of 27% under RCP45 and 56% under RCP85, with future populations projected to be found at higher elevations (459 and 676 m for RCP45 and RCP85 respectively). The distribution of *F. sylvatica* sl in Greece is projected to be significantly affected with a shrinkage up to 81 and 86% for the mild and extreme climate scenario.

Table 2: Summary of the spatial metrics used to compare the future (two scenarios) to current potential distribution of the seven study species.

<table>
<thead>
<tr>
<th>Habitat Availability</th>
<th>Pinus halepensis &amp; Pinus brutia</th>
<th>Pinus nigra cephalonica</th>
<th>Abies cephalonica</th>
<th>Quercus pubescens</th>
<th>Quercus frainetto</th>
<th>Fagus sylvatica</th>
</tr>
</thead>
<tbody>
<tr>
<td>BL vs 45</td>
<td>0.95</td>
<td>0.21</td>
<td>0.05</td>
<td>0.58</td>
<td>0.73</td>
<td>0.19</td>
</tr>
<tr>
<td>BL vs 85</td>
<td>1.11</td>
<td>0.16</td>
<td>0.02</td>
<td>0.50</td>
<td>0.44</td>
<td>0.14</td>
</tr>
<tr>
<td>Common Area</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BL &amp; 45</td>
<td>0.96</td>
<td>1.00</td>
<td>0.94</td>
<td>0.98</td>
<td>0.49</td>
<td>1.00</td>
</tr>
<tr>
<td>BL &amp; 85</td>
<td>0.86</td>
<td>0.99</td>
<td>0.69</td>
<td>0.98</td>
<td>0.37</td>
<td>1.00</td>
</tr>
<tr>
<td>Elevational Shift (m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RCP45</td>
<td>3</td>
<td>86</td>
<td>454</td>
<td>33</td>
<td>459</td>
<td>111</td>
</tr>
<tr>
<td>RCP85</td>
<td>79</td>
<td>367</td>
<td>705</td>
<td>231</td>
<td>676</td>
<td>324</td>
</tr>
</tbody>
</table>

Maps of these projection are given in Fig. 1 for conifers and Fig. 2 for broadleaved species. The expansion of the low-elevation pines is clear as well as the shrinkage in the potential distribution of the two higher elevation conifers. On the other hand, the potential distribution area of *Q. pubescens* seems to be located mainly at the western and wetter part of the country, while *Q. frainetto* potential distribution seems to move northwards and at higher elevations. The future distribution of *F. sylvatica* in Greece is projected to be mainly found across the higher elevations of the Pindos mountain range.

Conclusions

Overall our findings suggest that climate change might lead to significant shifts in the potential distribution of the study species. As these species represent key elements of Greek forest ecosystems, and thus our findings might be useful for inferring the vulnerability of this sector and its potential for adaptation under warmer future conditions.

From the seven study species, only the two low-elevation pines showed stable/expanding distributions under both climate change scenarios. These drought-tolerant species could potential inhabit areas that are currently not favourable for them and/or where are currently outcompeted by less drought-tolerant
species. Our projections yielded a small elevational shift of ca 80 m under the warmer future scenario. Across Greece, vegetation zones just above the current area of expansion of *P. halepensis* and *P. brutia* are frequently dominated by less drought-tolerant broadleaved species which might experience increased drought stress under warmer conditions, and thus retreat and free up space for pines. However, *P. brutia* and *P. halepensis* forests are in general less productive and provide lower quality wood which apart from some use in traditional fishing-ship building, it is rarely used for timber production. In addition to the above, stands dominated by these two pine species are more flammable due to their higher resin content compared to broadleaved species. Thus, in conjunction to the expected expansion of the high fire-risk period in Mediterranean regions, such vegetation shifts might lead to positive feedbacks (Fyllas and Troumbis 2009) that extent of fire prone areas.

*Pinus nigra* forests represent a European priority habitat type included in Annex I of the Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora. Black pine can grow in a range of temperature and water availability conditions (Enescu et al. 2016) but many studies suggest that this species might be sensitive to prolonged drought both in terms of adequate regeneration (Fyllas et al. 2008) and growth (Linares and Tiscar 2010). Our projections suggest a strong shrinkage of the species potential distribution area, across the whole country. Of importance are also the projected decline (close to extinction) in the *Abies cephalonica* dominated forests, which represent an endemic habitat type in Greece. Currently the Greek fir is found at the upper slopes of many mountains in the central and southern part of the country and thus it seems that under climate change the bioclimatically required > 450m elevation shift could not be realised, just due to topographic constrains (Fig 1a). It should be noted that apart from their ecological importance these two conifer species currently cover areas of significant timber production.

*Quercus pubescens* and *Quercus frainetto* are two of the more common oak species in Greece, currently found at lower to mid and mid-high elevations. *Q. pubescens* is a semi-deciduous species that can withstand water limitation. Recent studies show that it can be as tolerant to drought stress as evergreen oaks like *Quercus ilex* (Früchtenicht et al. 2018). Currently the species distribution spans across the country while our projections under climate change suggest a retreat of its populations in the western and north-eastern part by 2070, with a relatively modest elevation shift (+33m) under RCP45 and a stronger shift (+231 m) under RCP85 (Fig. 1b). *Q. frainetto* is used for both firewood and timber in combination with livestock grazing (Mauri et al. 2016). It is considered a native species in south-eastern Europe and is mainly found at the zone above the typical Mediterranean climate. It is a deciduous relatively tolerant species to water limitation but not as tolerant as other typical Mediterranean oaks such as *Quercus coccifera* and *Q. ilex*. The growth of *Q. frainetto* is positively related with the total amount of summer precipitation (Fyllas et al. 2017) and thus declines in summer water availability could negatively affect this species. Our projections suggest that under climate change the potential distribution of *Q. frainetto* could be moving northwards (Fig. 1b). *Fagus sylvatica* (beech) is one of the most abundant broadleaved species across Europe and it is extensively used in forest transition strategies (Gebler et a. 2007). However, the species is known to be sensitive to low water availability and drought (Fotelli et al. 2002) with its long-term growth also related to summer water availability (Fyllas et al. 2017). Our projections suggest a strong decrease of its distribution range under both climate scenarios and an associated elevation shift from 111 to 324 m, in agreement with other models that suggest that the species has the potential to expand its northern edge and loose habitat at the southern edge of its distribution in a future climate (Kramer et al. 2009).
Overall our findings illustrate that out of the seven study species only the two drought tolerant pines could potentially expand their distribution under future conditions. Significant reductions in the range of potential distribution of all other species could have important ecological, economic and social impacts, and thus adequate mitigation measures should be implemented.

Reference


Figures

Figure 1a: Projected current and future distribution of the four conifer species in Greece. The distribution of P. brutia is aggregated with that of P. halepensis due to similar ecological requirements.
Figure 1b: Projected current and future distribution of the three broadleaved species in Greece.

Q. pubescens BaseLine  Q. pubescens RCP45 @ 2070  Q. pubescens RCP85 @ 2070

Q. frainetto BaseLine  Q. frainetto RCP45 @ 2070  Q. frainetto RCP85 @ 2070

F. sylvatica BaseLine  F. sylvatica RCP45 @ 2070  F. sylvatica RCP85 @ 2070