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Predicting species dominance shifts across elevation gradient at mountain forests in Greece under a warmer and drier climate.

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Abstract

The Mediterranean Basin is expected to face warmer and drier conditions in the coming decades, following projected increases in temperature and declines in precipitation. The aim of this study is to explore how forests dominated by *Abies borisii-regis, Abies cephalonica, Fagus sylvatica, Pinus nigra* and *Quercus frainetto* will respond under such conditions. We combined an individual-based model (GREFOS), with a novel tree-ring dataset in order to constrain tree-diameter growth and to account for inter- and intra- specific growth variability. We used wood density data to infer tree longevity, taking again into account inter- and intra- specific variability. The model was applied at three 500m wide elevation gradients at Taygetos in Peloponnese, at Agrafa on Southern Pindos and at Valia Kalda on Northern Pindos in Greece. Simulations adequately represented species distribution and abundance across the elevation gradients under current climate. We subsequently used the model to estimate species and functional trait shifts under warmer and drier future conditions based on the IPCC A1B scenario. In all three sites, a retreat of less drought-tolerant species and an upward shift of more drought-tolerant species were simulated. These shifts were also associated with changes in two key functional traits, in particular maximum radial growth and wood density. Drought-tolerant species presented an increase of their average maximal growth and decrease of their average wood density, in contrast to less drought-tolerant species.

Introduction

In areas surrounding the Mediterranean basin, forests are an important element of the established vegetation, covering around 20-30% of the total land areas in the northern part and reaching up to 50% in Greece (Archibold 1995; Scarascia-Mugnozza et al. 2000). These forests are expected to experience warmer and drier conditions in the near future due to global warming (Giorgi and Lionello 2008; Gualdi et al. 2013), as well as potential shifts in fire frequency driven by both climatic and anthropogenic forcing (Barbero et al. 1990; Pausas 2004; Moriondo et al. 2006). Observational evidence of shifts in forest structure and function over the last century has started to accumulate and are usually attributed to climatic changes. Tree-growth changes related to temperature increase (Jump et al. 2006; Linares and Tiscar 2010), decline in precipitation (Sarris et al. 2011), and/or CO_2 fertilisation (Martinez Vilalta et al. 2008) have been documented at both low and high elevations around the Mediterranean region. Forest dieback has been attributed to drought (Van Mantgem et al. 2009; Allen et al. 2010,) and/or to pathogens outbreaks (Desprez-Loustau et al. 2006; Chrysopolitou et al. 2013), while drought-induced changes in species composition have also been reported (Allen and Breshears 1998; Penuelas and Boada 2003). Furthermore, some studies report an increase in fire frequency associated with the recent warming, both in the north-western (Pausas and Fernandez-Munoz 2012) and the north-eastern (Koutsias et al. 2013) part of the Mediterranean Basin. The way these shifts will progress under future global change conditions is important in terms of nature conservation and climate change adaptation (Bonan 2008).

Mediterranean plants have evolved under low water availability and thus have developed a number of morphological and physiological adaptations that enable them to withstand prolonged drought periods (Sardans and Penuelas 2013). Recent studies suggest in Mediterranean climate there is a continuum of plant drought performance, ranging from fast-growing deciduous species with a high resource-use and high drought vulnerability to conservative slow-growing evergreen species with low water-use and high drought tolerance (Lopez-Iglesias et al. 2014). The two ends of the spectrum reflect a drought-tolerance versus a drought-avoidance strategy, and functional traits such as rooting depth per leaf area, relative growth rate and net assimilation rate were found to be good predictors of seedling drought survival time (Lopez-Iglesias et al. 2014). Seedlings of fast growing species were less drought-tolerant in contrast to slow-growing species that exhibited a higher drought tolerance. A similar (weak) trade-off between growth and survival has been reported for mature trees with wood density being a good (negative) predictor of relative growth rate (Martinez-Vilalta et al. 2010). The above suggest that based on their functional configuration Mediterranean species are responding individualistically to drought and thus their distribution could be controlled by water availability (Piedallu et al. 2013).

Simulations from both local and global scale vegetation models suggest that forests established under Mediterranean climate are particularly vulnerable to climate change (Morales et al. 2007; Fyllas and Troumbis 2009; Hickler et al. 2012), although the large climatic stochasticity of Mediterranean ecosystems (Blondel and Aronson 1999) could increase the uncertainty in such modelling exercises. Under climate change conditions, some typical Mediterranean forests dominated by species like *Pinus halepensis* are projected to be more resilient than others that are mainly found in the temperate zone (Keenan et al. 2011). One of the key drivers of vegetation and/or productivity shifts in these predictions is the increased soil moisture deficits, following an increase in temperature and a decrease in precipitation under climate change (Morales et al. 2007). However, other factors, such as fire frequency and CO_2 fertilisation could also interact with water limitation leading to complex ecosystem responses (Fyllas and Troumbis 2009; Keenan et al. 2011). Disentangling the role of water limitation, fire and CO_2 in forest ecosystem processes is important in order for their current dynamics and future risks to be better understood. Field studies, specifically designed to constrain the way such processes are simulated in vegetation dynamics models, could increase our understanding of forest function under current conditions and enhance our confidence in the projections of their future state.

In addition to the above, the role of inter- and intra- specific functional trait variation has been recently highlighted as an important component that needs to be incorporated into vegetation dynamics model (Scheiter et al. 2013; Fyllas et al. 2014; van Bodegom et al. 2014; Sakschewski et al. 2015). Traditionally, parameterisation of species and/or plant functional types (PFTs) is based on the use of some "average" or "appropriate" mean trait value, for characteristics that have a direct effect on the regeneration, the growth and the mortality of the simulated individuals. For example specific leaf area has been used as a parameter to differentiate the turnover rate of leaf biomass between PFTs (Sitch et al. 2008), or as a parameter to describe the architecture (in terms of foliage area/biomass) of different tree species (Bugmann et al. 2001; Fyllas et al. 2007). The selection of one "average" trait value could lead to "static" model behaviour as the population variability in the response of species/PFTs is *a priori* restricted, just because of the constant value given to some key functional characters (Fyllas et al. 2012; 2014). Ignoring the intra-specific variability is not in agreement with what is observed in real plant communities and comprises a key element of natural selection and evolution. In addition, depending on the way vegetation dynamics models are built, variability in some functional characters could affect more than one simulated process, through either direct or indirect routes. For example, given that most vegetation dynamics models include a "carbon-starvation” mortality term, the influence of a specific growth-parameter on model behaviour could be manifested directly through growth and indirectly through mortality. Ignoring functional variation in simulated plant communities could be an important bias, especially when projecting vegetation dynamics under climate change conditions, where alternative "functional configurations" could lead to viable life strategies.

Individual-based modelling is a tool widely used to simulate vegetation dynamics (Grimm et al. 2006). Forest gap-dynamics models are a special group of individual-based models that follow the life of each tree in a stand and simulate key processes of interest like regeneration, competition and mortality (Bugmann 2001). Gap-dynamics models have a long history in modelling forest ecosystems structure and function with applications all over the world (Shugart 1984; Bugmann 2001; Fyllas et al. 2007; Ngugi et al. 2013). Because these models are based on empirical equations of growth and mortality, they provide reasonable approximations of stand growth, succession and disturbance patterns. Furthermore, as these models focus on individual-tree performance, they provide an excellent framework to consider intraspecific trait variability and explore the potential shifts in species or community level trait-variation under changing environmental conditions. However, to our knowledge there is no study that incorporates trait variability in the widely used forest-gap dynamics modelling framework.

In this study we combine the GREFOS forest-gap dynamics model (Fyllas et al. 2007, Fyllas and Troumbis 2009) with a novel tree-ring width and wood density dataset to account for growth and mortality intra-specific variability in simulations of forest dynamics, and to explore for potential shifts in species composition and functional traits under warmer and drier conditions. In particular using the tree-ring width dataset we initially derive species-specific diameter growth curves. We also use the observed inter- and intra- variability in wood density to infer individual tree longevity. In addition, by combining the tree-ring width and wood density datasets, we identify a growth versus longevity trade-off that is subsequently incorporated in the model by hardwiring a relationship between two key functional traits, i.e. the maximum diameter growth (G_m) and the wood density (D_W). We then apply the model across three 500m long elevation gradients in mountainous areas in Greece to:

1) Evaluate the predictive ability of the model and compare the “static” (single trait values) versus the “plastic” (varying trait values) model setup under current climatic conditions.
2) Explore how the species composition and functional variation of these forests will respond to a gradually warmer and drier climate.

Materials & Methods

Study Sites and Dominant Tree Species

Three study areas (Fig. 1) were selected to parameterise the model and validate its predictive ability. In each study area three 30x30 m^2 plots have been established as part of the Mediterranean Forests in Transition (MEDIT) project, where a suite of plant functional traits and tree-ring width data have systematically been measured. Soil texture and depth are also available for each plot. In each plot all trees above 1 m have been identified and the diameter at breast height has been measured for all trees above 1.3 m. In all areas the plots are found across an altitudinal range of ca 500 m (Table 1). The first study area is located in the southern part of Mount Taygetos, Peloponnese. *Pinus nigra* and *Abies cephalonica* are the dominant tree species in this area, with the pine dominating the lower elevations and the more disturbed sites of the region. Soils are rather shallow with a high sand content (sandy loam). Mean annual temperatures range between 9.2 and 13.1 ^oC and annual precipitation between 850 and 950 mm. The second study area, the driest of the three, is located in the Agrafa region, Southern Pindos and it is dominated by *Quercus frainetto* at lower elevations and

Abies borisii-regis at higher altitudes. At lower altitudes soil is sandy clay loam shifting to clay loam at higher elevation. Across this elevation gradient mean annual temperature ranges from 10.3 to 14.2 ^{o}C and annual precipitation from 775 to 864 mm. The last study area, the wettest of the three, is found in the Northern part of the Pindos range and the dominant species are *Pinus nigra* and *Fagus sylvativa*, with the beech restricted at higher altitudes. Soils are deeper here with higher silt content (sandy loam). Temperature ranges from 7.6 to 9.7 ^{o}C and precipitation from 926 to 962 mm per year. At Mt Taygetos in *P. nigra* dominated stands 11 surface fires have been recorded over the last 165 years (Christopoulou et al. 2013), while in *P. nigra* dominated stands at Pindos North (Valia Kaldas) fire frequency is likely lower with 8 fires recorded over a period of 815 years (Touchan et al. 2012).

Model Description

A detailed description of GREFOS model is provided elsewhere (Fyllas et al. 2007). The model has been developed, parameterised and used for forest species found in the north-eastern part of the Mediterranean area (Fyllas et al. 2007; Fyllas and Troumbis 2009; Fyllas et al. 2010; Kint et al. 2014). GREFOS takes into account the discrete life history strategies (LHS) of Mediterranean tree and shrub species (Pausas 1999), by assigning a distinct recruitment density and resprouting capacity to each LHS. **Regeneration** in the model is based on empirical relationships between stand-level LAI and recruitment density (Fyllas et al. 2008; Fyllas et al. 2010), where a maximum threshold of LAI "ceases" the establishment of saplings through light limitation. Individuals are **competing** for light through a height-based hierarchy with taller trees shading all smaller ones. A daily soil water balance model is used to calculate relative water content (ϑ) and subsequently the annual drought duration in order to adjust growth (Granier et al. 1999; Fyllas and Troumbis 2009). Evaporation is estimated following the Priestley-Taylor (1972) method, while the pedotransfer functions of Wosten et al. (1999), along with site-specific soil texture and depth measurements, are used to calculate soil water retention and release parameters.

As in most forest-gap dynamics models, annual tree **growth** is estimated through the concept of optimum diameter increment, i.e. the growth that an individual of a certain species and size can reach under no-resource limitation or competition (Moore 1989; Bragg 2001; Risch et al. 2005). The "actual" diameter increment is subsequently estimated by adjusting the optimum diameter growth, as a function of the abiotic (temperature & water availability) and biotic (shading) conditions that prevailed for a given time for each tree in the stand. Here we use a novel ring-width data to estimate the parameters (and their variation) of a commonly used optimum growth equation (Zeide 1993), as described in the “Optimum growth curve and intraspecific plasticity” section.

Mortality has three components. The growth related component ("carbon starvation") estimated as a function of a tree's past growth, the background (“intrinsic”) mortality representing species longevity, and the fire related mortality, which is linked to species LHS. Background mortality is usually estimated in forest-gap models through species longevity or maximum size. Here we use wood density as a proxy for background mortality (Martinez-Vilalta et al. 2010). Intra- and inter- specific variation in wood density is incorporated in the model based on a novel wood density dataset, as described in the “Background Mortality” section. Species with a higher wood density generally have lower growth and mortality rates (Reich 2014). This growth versus survival trade-off has been incorporated in the model by hardwiring a relationship between maximum diameter growth rate and wood density based on the combined analysis of the tree-ring width and wood density datasets (“Growth – Longevity Trade-off” section).

Optimum growth curve and intraspecific plasticity

In order to parameterise the diameter growth curve a minimum of twenty tree cores were taken from each dominant species at each study area. All cores were collected at breast height with a 5 mm increment borer. In the lab, the cores were glued on channelled wood, dried at room temperature, and sanded with progressively finer grade abrasive paper until cells were clearly visible under magnification. All samples were visually cross-dated using visual recognition of tree-ring patterns and lists of marker years (those with narrow rings) (Yamaguchi 1991). Tree-ring widths were measured to 0.01 mm using Time Series Analysis and Presentation (TSAP) software package and LINTAB measuring table. Raw ring-width series were synchronized according to their Gleichläufigkeit score, which represents the overall accordance of two series t-values, which are sensitive to extreme values such as marker years and the cross-date index (CDI), which is a combination of both (Rinn2003). Finally, the COFECHA software was used to perform a data quality control and to evaluate the cross-dating (Grissino-Mayer 2001).

These data were subsequently used to estimate the parameters of an optimum growth curve (Zeide 1993). We considered optimum growth to be species specific, and thus we estimated the parameters of the curve for each species using data from all available sites. As in Bragg (2001), we assume that individuals growing at the highest rate for a given diameter class provide an adequate estimate of size-specific optimal growth. In this version of the model the optimum growth of an individual is described by the equation (Zeide 1993):

$$g = G_m e^{-0.5\left(\frac{\log\frac{D}{D_o}}{D_b}\right)^2} \quad (1)$$

where G_m is the maximum radial growth rate (mm a^{-1}) at the peak of the log-normal growth curve, D_o is the diameter at breast height (D) associated with the maximum growth rate, and D_b determines the width of the curve.

We fitted non-linear least square regression models using the R programming language and the *nls* library (R Development Core Team 2015) to estimate the species-specific G_m, D_o and D_b along with their confidence intervals (Table 2). In order to account for intra-specific growth variability in the model ("plastic setup"), a normal distribution is used to randomly assign the growth parameters for each tree of a certain species using the parameter estimates in Table 2. The first generation of simulated trees are randomly initialized based a normal distribution that follows our observations. Subsequent generations inherit growth characteristics from a normal distribution that is updated each year based on the parameters of the surviving trees.

Background mortality

The background mortality component (Π_R) was parameterised based on the equation reported in Martinez Vilalta et al. (2010), for tree species found in Spain under a similar range of climatic conditions:

$$\Pi_R = 0.51e^{(-3.56 \, x D_W)} \quad (2)$$

where wood density (D_W [g cm^{-3}]) is considered the main predictor of annual background mortality rate.

We collected stem wood samples from individuals within our study sites to estimate species-specific wood density values along with their confidence intervals. D_W was calculated for each sample using the water-displacement method. A container was filled with water and placed on a digital balance. A dried wood sample (48h at 60oC) that was weighted beforehand was then sunk into the container until completely immersed. The volume of the wood sample was estimated from the water displacement. Similar to growth the inclusion of intraspecific variability for mortality in the model was applied through a species-specific normal distribution with mean equal to DW and standard deviation equal to D_{Wsd} (Table 3).

Growth – Longevity Trade-off

Species with higher wood density generally have lower growth and mortality rates (Reich 2014). This growth versus survival trade-off has been incorporated in the model by hardwiring a relationship between maximum radial growth rate and wood density, based on the analysis of the entire MEDIT dataset (Fyllas et al. unpublished data). To derive the $G_m=f(D_W)$ relationship we analysed tree-ring width and wood density data for 9 species in 35 plots across Greece. In this analysis the optimum growth curve (equation 1) was fit with non-linear least square regression models for all individual of a tree species at site. Then the species and sites specific G_m, D_o and D_b estimates were regressed against the average D_W of each species at each site. A statistically significant relationship was identified only for G_m and D_W (Figure 2), with G_m decreasing with D_W and supporting the hypothesis of a growth – longevity trade-off. It should be noted that this relationship holds only across species, as the number of samples available was not adequate to validate it within species.

Simulation Setup

At each study area the model was set up to simulate stand dynamics along an altitudinal (500 m wide) gradient, with an elevation step of 50 m. Soil depth was set to 2.0 m in all study sites. All simulations started from bare ground and lasted for a 1000-year-long simulation period. In this study the fire component of the model has been disabled in order to explore for merely the effects of drought. At each study site only the two species known to occur abundantly are allowed to establish. It should be noted that these two species are the dominant elements of vegetation accounting for more than 80% of the total basal area in our study plots. Two climate scenarios were used, namely: 1) the baseline (BL) climate representing the current climatic conditions with the climate of the 20th century at each study area randomly repeated for the simulation period, and 2) the IPCC A1B climate change (CC) scenario with an approximately 3^{o}C increase in temperature and 20% reduction in precipitation taken as one of the intermediate projections cases from an ensemble regional climate model projections for the Mediterranean area (Gualdi et al. 2013). The baseline climate was extracted from the E-OBS gridded climatology (Haylock et al. 2008) for the time period between 1950 to 2013. Across the elevation gradients, temperature was corrected with a lapse rate of 6.5 ^{o}C/km. Precipitation was assumed not to change with elevation. In both cases a spin-up period of 500 years, during which the observed 1950-2013 climate was randomly replicated, was used until vegetation reached an equilibrium with climate. For the CC scenario during the spin-up period, climate was assumed to be similar to BL conditions, followed by a transient period of 100 years during which temperature and precipitation anomalies were linearly applied until climate stabilized after year 600.

The model was applied following a “static” (no intraspecific variability) and “plastic” (with intraspecific variability) setup, and 30 iterations were performed for each elevation and climate scenario. The steady state (year: 600-1000) average basal area of each species under baseline conditions was estimated and compared with local observations. Changes in the species average values of the two key traits, G_m and D_W, with time and climate scenario were also explored. Potential shifts in these traits indicate the way species could adapt to warmer and drier conditions, by adjusting the two traits that are directly linked to their growth and mortality.

Results

Simulations under baseline conditions adequately captured the ranges of species distribution across the elevational gradient of the three study sites. At Mt. Taygetos, *P. nigra* is more abundant at lower elevations, while *A. cephalonica* increases its contribution with altitude (Fig. 3 – left panel). Simulated basal area was reasonably well estimated for *P. nigra* but underestimated for *A. cephalonica* in both the “static” and the “plastic” model setup (Fig. SM1). The “static” model setup yielded a higher *P. nigra* abundance compared to the “plastic” setup across all altitudes, while *A. cephalonica* achieved a higher basal area under the “plastic” setup (Fig. SM1). Following the climate change scenario, the model simulated an uphill shift of *P. nigra* across the whole altitudinal gradient and a significant decrease of *A. cephalonica* using the plastic model setup (Fig. 3 – right panel). The decrease of *A. cephalonica* was stronger under the static model parameterisation (Fig. SM2)

At Agrafa in the southern part of Pindos, under BL conditions *Q. frainetto* is more abundant at lower elevations, but with increasing altitude *A. borisii-regis* becomes the dominant element of vegetation (Fig. 4 – left panel). Simulated basal area was reasonably estimated for both species especially under the “plastic” model setup (Fig. SM3). The applied climate change scenario leads to a total replacement of the *A. borisii-regis* by *Q. frainetto* across the elevation gradient of this area using the plastic (Fig. 4 - right panel) traits parameterisation. The inclusion of trait plasticity did not yield simulation of better *A. borisii-regis* performance under CC condition and a complete replacement by *Q. frainetto* was also simulated (Fig. SM4).

At Valia Kalda in the northern part of Pindos, the observed vegetation transition with elevation was realistically replicated under BL conditions. *P. nigra* dominates the stands at lower elevations while *F. sylvatica* is more abundant at elevations above 1350m (Fig. 5). The steady state standing basal area was accurately simulated for both species, with small differences between the static and the plastic parameterisation (Fig. SM5). At this region, CC simulations suggest a complete replacement of *F. sylvatica* by *P. nigra* across the simulated elevation gradient using both the plastic (Fig. 5) and the static model setup (Fig. SM6).

We additionally explored for potential shifts in the key traits that were used to predict growth and mortality of the four tree species, i.e. maximum growth rate (G_m) and wood density (D_W). The long-term trends of the average G_m and D_W for each study area across elevation is presented in the Supplementary Material (Fig. SM7 to SM12). In general under current conditions, average species D_W decreased and G_m increased with time, suggesting that individuals with greater growth are performing better, and thus drive the average trait values of the stand. The same trend was also observed in CC simulations with some shifts in the average species trait values. The steady state average values of G_m and D_W under BL and CC conditions are summarised in Figs 6, 7 and 8.

At Mt. Taygetos, *P. nigra*'s average wood density and maximum growth showed no clear trend with elevation (Fig. 6). Under climate change conditions, an overall small decrease in $D_{W,}$ associated with an increase in G_m for *P. nigra,* was simulated. For *A. cephalonica* a small decrease of D_W with elevation was simulated, especially under BL conditions. At Agrafa, D_W increased and G_m decreased with altitude for the more drought-tolerant *Q. frainetto* under BL conditions. This trend was not as strong under CC conditions (Fig. 7). No clear trend in D_W or G_m was simulated for *A. borisii-regis* although at higher altitudes the average D_W value was smaller compared to lower altitudes. At Valia Kalda (Fig. 8), the elevational shifts of simulated D_W and G_m with altitude were more pronounced. A lower G_m and a higher D_W were achieved at higher altitudes for the more drought tolerant *P. nigra*, with the opposite trend found for *F. sylvatica.* Overall G_m increased and D_W decreased under CC conditions for the more drought-tolerant species, while the opposite was true (decreasing G_m and increasing D_W) for the less drought-tolerant species across all sites.

Discussion

This study presents the parameterisation of a forest-gap model, with novel tree-ring width and wood density measurements, aiming to better understand and to project the dynamics of typical mountainous forests in Greece. The inclusion of species-specific parameters leads to an realistic prediction of the distribution patterns and the basal area of the dominant tree species, observed in three study sites under current climate. In general the predicted steady state average basal area is accurately simulated for lower altitudes and early successional species, but was slightly underestimated at higher altitudes and late successional species. By accounting for intraspecific variability in growth and mortality through two functional traits (maximum growth rate and wood density) the model simulates a higher contribution of slow-growing species across all altitudes. We suggest that vegetation dynamics models, and particularly those that are implemented at local scales, should be constrained with site-specific information that takes into account the variability of key functional traits.

The inclusion of growth and mortality plasticity is an important aspect of this work. Currently there is great effort to include functional trait variation into vegetation dynamics models, in order to account for the potential plasticity in the ecosystems' response to climate change (Scheiter et al. 2013; Fyllas et al. 2014; van Bodegom et al. 2014). In this study we present a simple method to implement trait variation within existing forest gap-dynamics models, based on the measured intra-specific variability in functional traits associated to tree growth and longevity. Our approach is based on the inclusion of a fundamental trade-off between growth and survival. Wood density is selected as the core trait to represent this trade-off. Lower wood density is related to higher growth and mortality rates both within and between the species of interest. On the other hand, higher wood density is associated with smaller maximum growth and mortality rates. By parameterising this theoretical trade-off with species-specific measurements of tree growth and wood density the model adequately captures the vegetation dynamics in our three study sites. Additional axes of functional trait variation that represent ecophysiological trade-offs could be potentially integrated in this modelling framework in future studies. These could relate to species hydraulic properties and/or response to disturbance (Pausas 1999, Sánchez-Gómez et al 2006).

In all study sites CC simulations suggest an upward shift in the dominance patterns, with more drought-tolerant species (*Pinus nigra* and *Quercus frainetto*) increasing its contribution at higher altitudes. The inclusion of trait plasticity does not significantly alter the CC simulations outcomes, with the only exception at Mt Taygetos, where the *A. cephalonica* was more persistent at higher altitudes when the trait plasticity was included. The overall trend of shifting dominance patterns with CC is related to the drought tolerance of the studied species. Compared to *A. borisii-regis* and *F. sylvatica*, the higher elevation dominant species at South and North Pindos, *A. cephalonica* is considered more drought-tolerant and thus it maintains its contribution to the stand's basal area under CC conditions. It should be noted that species response to drought is simulated in this version of the model by counting the number of days with water stress that feeds into a species-specific drought response function (Granier et al. 1999; Fyllas and Troumbis 2009). Hence there is no direct effect of trait plasticity to a species and/ or individual's drought tolerance. Various studies suggest a relationship between cavitation resistance (Hacke et al. 2001) and drought tolerance (Poorter and Markesteijn 2008; Preston et al. 2006; but see Hoffmann et al. 2011) with D_W, and thus such a relationship could be implemented in future versions of this modelling framework.

In this study simulated shifts in species dominance were also associated with changes in the two functional traits used to describe variation in growth and mortality. In all three study sites the CC scenario resulted in higher G_m of the drought-tolerant species (*P. nigra* and *Q. frainetto*) and lower D_w. Shifts in G_m and D_w were not as clear for the less drought-tolerant species, with the exception of *F. sylvatica* at North Pindos, where a systematic decrease in G_m and increase in D_w was simulated. These outputs suggest that across the studied elevation gradients, species that are able to tolerate longer dry periods could increase their growth rate in contrast to less drought tolerant species. It should be noted that our modeling framework is not only taking into account the uncertainty of vegetation processes (Reyer et al. 2016) by including variation in growth and mortality, but also enables tree populations to shift their functional characteristics. This is particularly important in terms of adaptation to changing biotic and abiotic conditions.

Empirical evidence of species upward shifts (Penuelas and Boada 2003; Moser et al. 2010; Pauli et al. 2012) have been documented and modelling exercises identify the vulnerability of Mediterranean ecosystems to climate change (Morales et al. 2007; Fyllas and Troumbis 2009; Hickler et al. 2012). Simulations in this study suggest that climate change could lead to significant shifts of species distribution in mountainous Mediterranean forests. The importance of considering intraspecific variability for modelling purposes is highlighted here. Although in two of the study sites incorporating trait variability did not "enhance" the ability of the least drought-tolerant species to adapt to a changing climate, in Mt Taygetos the response of *A. cephalonica* to drier conditions was more gradual under the plastic model setup. Such responses will be dependent on local environmental conditions as well as the ecophysiological ranges of species performance. Field studies that quantify these ranges as well as the way functional traits coordinate and interact to form fundamental ecological strategies could help us better parameterize models of vegetation dynamics.

Conclusions

This study presents the application of a forest gap dynamics model to explore the potential effects of drought on the dynamics of mountainous Mediterranean forests in Greece. Emphasis was given on incorporating intra-specific variability in growth and mortality. Simulations under climate change conditions suggest an upward shift of the more drought-tolerant species. These changes are also accompanied by intraspecific shifts in two key functional traits that express the growth and mortality patterns of the tree species. In general, populations of more drought-tolerant species increase their maximum radial growth and decreased their wood density in contrast to less drought-tolerant species. Incorporating trait variability and accounting for fundamental ecological trade-offs in vegetation dynamics models could increase the realism in projecting the fate of forest ecosystems under global change conditions.

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