



Mediterranean Forests in Transition (MEDIT): Deliverable No9

Title: Report on small scale simulation results

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Summary

This report presents the findings of work done in Work Package 6, activity 6.1 of the MEDIT Project entitled "Small scale simulations of forest dynamics under baseline and climate change conditions". This is an integration of work made in different Working Packages (WPs) and in particular brings together the developments of the small scale GREFOS model (in WP2 and WP6), the tree rings analysis (WP1 and WP4) and the functional traits data measured (in WP4) and analysed (in WP5). The scientific aim of this deliverable is to identify potential shifts in the dynamics of some Mediterranean forest to climate change. The working model is the GREFOS forest gap dynamics simulator as further developed and parameterised during the MEDIT project.

Introduction

At areas surrounding the Mediterranean basin, forests are an important element of the established vegetation (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). Understanding their sensitivity and response under global change conditions is important for their management as well as for their conservation (Bonan 2008).

Vegetation dynamics models have been widely used as tools to project the response of ecosystems to changing environmental conditions (Prentice et al. 1993; Woodward and Loomas 2004; Sitch et al. 2008). A special group of such simulators are individual-based models that follow the life cycle of each plant in a community and simulate key processes of interest like regeneration, competition and mortality (Grimm et al. 2006). Gap-dynamics models have a long history in modelling

forest ecosystems structure and function, following an individual-based approach, with applications all over the world (Shugart 1984; Pacala et al. 1996; Bugmann 2001; Fyllas et al. 2007; Ngugi et al. 2013). Because most of the algorithms within these models are based on empirical equations, they provide reasonable approximations of growth, succession and disturbance patterns. However, caution should be given when extrapolating the results of such models under changing environmental conditions, as has already been noted (Loehle and LeBlanc 1996).

Simulations from both global and local scale vegetation models suggest that forest established at Mediterranean areas are particularly vulnerable to climatic changes (Morales et al. 2007; Fyllas and Troumbis 2009; Hickler et al. 2012), although the climatic stochasticity of Mediterranean ecosystems (Blondel and Aronson 1999) could increase the uncertainty in such modelling exercises. Under climate change simulations, some typical Mediterranean tree species like *Pinus halepensis* are projected to be more tolerant than others that are mainly found at the temperate zone (Keenan et al. 2011). One of the key drivers of vegetation and/or productivity shifts in these approaches is the increased drought stress, following an increase in temperature and decrease in precipitation under projected climate change conditions (Morales et al. 2007). However, other factors, such as fire frequency and CO₂ 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 CO₂ on Mediterranean forest is important in order to better understand their current and future dynamics. Field and laboratory 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 results of their simulated future states.

Recently the role of functional diversity at the community level and the role of functional trait variation at the species level have been highlighted as important components 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) are 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 (SLA) 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 differentiate between the architecture (in terms of foliage area/biomass) between tree species (Bugmann et al. 2001; Fyllas et al. 2007). The selection of one "average" trait value could lead to a

"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 to what is observed at 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 processes, 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 the growth algorithm and indirectly through the mortality algorithm. Ignoring 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.

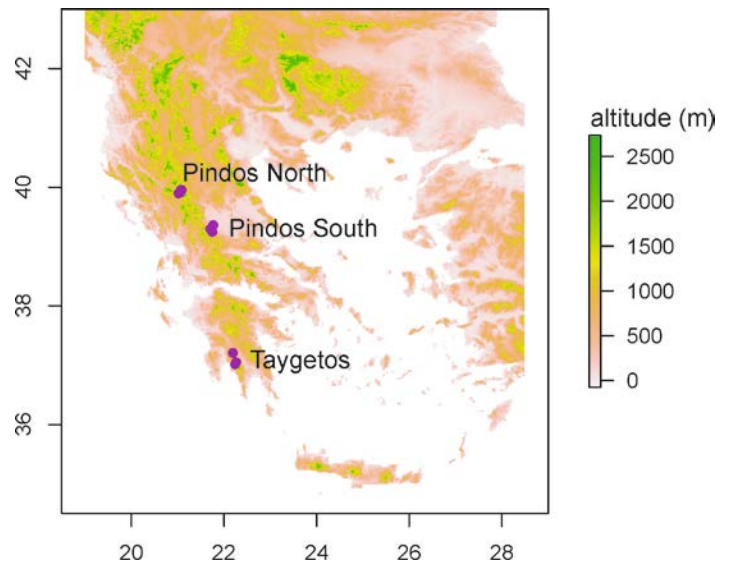
In this study we incorporate growth and mortality intra-specific variability in simulations of forest dynamics to evaluate the vulnerability of typical forests found in Greece to drought. To do that we combine the "Greek Forest Species Simulator", GREFOS, with a tree ring-width and wood density dataset from cores taken at three study areas. The GREFOS model has been developed, parameterised and used for forest species found at the north-eastern part of the Mediterranean area (Fyllas et al. 2007; Fyllas and Troumbis 2009; Fyllas et al. 2010; Kint et al. 2014). In most forest-gap dynamics models, annual tree growth is usually estimated through the concept of optimum diameter increment, i.e. the diameter growth that an individual of a certain species and size would achieve 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 based on the abiotic and biotic conditions that prevailed for a given time and individual within the stand. Here we use ring-width data in order to estimate the parameters (and their variation) of a commonly used optimum growth equation (Zeide 1993). Variation in optimum growth between individuals of the same species is then included by using a distribution of the growth curve parameters instead of static values. Background mortality is usually estimated in forest gap models through species longevity. Here we use wood density as a proxy for background mortality (Martinez-Vilalta et al. 2010) and again include intra-specific variability through the estimated variation from our samples. Species with a higher wood density are in general considered to present a smaller growth rate and a lower annual death probability (Reich 2014).

The aim of this paper is to explore the vulnerability of three common forest types in Greece to climate change. We applied the GREFOS model at three different geographic regions along an altitudinal gradient of 500 m. Two climatic scenarios were used to force the model under current (BL - BaseLine) and climate change (CC - IPCC A1B) conditions, and model outputs were comparatively considered. The probabilistic algorithm of van Oijen et al. (2013) was subsequently applied to determine the vulnerability of the simulated stands to climate change in terms of annual biomass production and species composition.

Materials & Methods

Study Sites and Dominant Tree Species

Three areas with different dominant tree species were selected to obtain the tree cores used in this study (Fig. 1). In all study areas the sampled trees were found across an altitudinal range of ca 500 m (Table 1). The first study area is located at the southern part of Mount Taygetos, Peloponnese. *Pinus nigra* and *Abies cephalonica* are the dominant tree species at this area, with the pine dominating the lower elevations and the more disturbed sites of the region.



The second study area is located at the Agrafa region, Southern Pindos and it is dominated by *Quercus frainetto* at lower elevations and *Abies borisii-regis* at higher altitudes. The last study area is found at the Northern Part of the Pindos range and the dominant species are *Pinus nigra* and *Fagus sylvatica*, with the beech restricted at higher altitudes.

Table 1. Study site description

Study Area	Mt Taygetos	Pindos South	Pindos North
Longitude	22.23	21.70	21.05
Latitude	37.01	39.35	39.91
Elevation Range (m asl)	795-1451	540-1087	1014-1470
Average Annual Temperature (°C)	11.3	13.3	8.4
Total Annual Precipitation (mm)	899	845	941
Dominant Species	<i>P. nigra</i> , <i>A. cephalonica</i>	<i>Q. frainetto</i> <i>A. borisii-regis</i>	<i>P. nigra</i> <i>F. sylvatica</i>

Model Description

A detailed description of the GREFOS model is provided elsewhere (Fyllas et al. 2007; Fyllas et al. 2010). In brief GREFOS is a forest gap-dynamics model that simulates the lifecycle of each tree in a stand. Individuals are competing for light through a height-based hierarchy with taller trees shading all smaller trees, and for water based on their belowground biomass. GREFOS accounts for the discrete life history strategies that have been identified for Mediterranean tree and shrub species (Pausas 1999). Fire seeders (ex. *Pinus brutia* and *Pinus halepensis*) have an increased recruitment rate and a low survival probability after a fire event. Seeders (ex. *Abies borisii-regis*, *Abies cephalonica* and *Pinus nigra*) have a sensitive to fire recruitment stage. *P. nigra* has a relatively higher survival probability (through thicker bark) during a fire. Most *Abies* species are not adapted to fire. Facultative resprouters (ex. *Fagus sylvatica*, *Quercus frainetto*) have an intermediate recruitment density and resprouting ability. Obligate resprouters (ex. *Quercus coccifera* and *Quercus ilex*) have a low recruitment density and a high resprouting efficiency. Regeneration in the model is based on empirical relationships between stand-level LAI and recruitment density (Fyllas et al. 2008; Fyllas et al. unpublished data), where a maximum threshold of LAI "ceases" the establishment of saplings, through light limitation. Mortality has three components. The growth related component ("carbon starvation") estimated as a function of a tree's previous past growth, the background mortality representing species longevity and estimated here as a function of wood density, and the fire related mortality which is linked to a species life history strategy and thus recruitment density and resprouting efficiency. Growth is parameterised through species-specific tree-ring width data as further explained in the following paragraph. 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). In this new version of the model, evaporation is estimated following the Priestley-Taylor (1972) method while the pedotransfer functions of Wosten et al. (1999; 2001) along with a user specified soil depth are used to calculate soil water retention and release parameters. Deeper soils provide higher water availability to the established trees. In this study the fire component of the model has been disabled in order to explore only for the effects of drought. The two processes of interest that were calibrated with data from trees measured at our study sites are individual tree growth and mortality. These are further explained below.

Optimum growth curve and intraspecific plasticity

In order to parameterise the growth algorithm a minimum of twenty tree cores were taken for each tree species at each study site. Sampled trees were selected to be found outside the stand and receiving the full amount of sunlight during a day. 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 (Rinn 2003). 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 the optimum growth curve, widely applied in many forest gap models. Here we consider optimum growth to be species specific, and we thus estimate the parameters of the curve for each species. 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 proposed by Zeide (1993):

$$g = g_m e^{-0.5 \left(\frac{\log \frac{D}{D_0}}{D_b} \right)^2} \quad (1)$$

where g_m is the maximum radial growth rate (mm a^{-1}) at the peak of the log-normal growth curve, D_0 is the diameter at breast height (D) associated with the maximum growth rate, and D_b determines the width of the curve.

The tree-rings data were used to estimate g_m , D_0 and D_b along with their confidence intervals. We fitted non-linear models using least square regressions with the use of the R programming language and the *nls* library (R Development Core Team 2015). Table 2 summarises the species-specific parameter estimates along with their standard deviations. In order to account for intra-specific growth variability in the model, a normal distribution is used to randomly assign the growth

parameters for each tree of a certain species. 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.

Table 2. Parameter estimates along with their confidence intervals for each study species.

Species	G_m (mm y^{-1})	G_m sd	D_o (cm)	D_o sd	D_b (-)	D_b sd
<i>Abies borisii-regis</i>	6.07	1.07	16.38	8.33	1.97	0.47
<i>Abies cephalonica</i>	5.48	1.09	9.57	4.71	1.72	0.88
<i>Fagus sylvatica</i>	3.46	1.46	8.84	5.78	2.09	0.80
<i>Pinus nigra</i>	5.34	1.14	7.53	2.83	1.53	0.56
<i>Quercus frainetto</i>	4.52	1.17	6.41	2.81	1.25	0.19

Background mortality

The mortality component (Π_R) of the model was parameterised based on the equation reported in Martinez Vilalta et al. (2010). This equation was developed for tree species found in Spain under a similar range of climatic conditions. It uses wood density (D_W [$g\ cm^{-3}$]) as a sole predictor. Here we use stem wood samples from individuals established within our study sites to estimate species specific wood density values along with their confidence intervals. After collecting samples from the field the water-displacement method was implemented to estimate D_W as it allows for easy and reliable volume measurement (Chave 2005). A container was filled with water and placed on a digital balance. A dried wood sample (48h at 60°C) that was weighted before hand was then sunk in the container, such that it is completely immersed. The volume of the wood sample is estimated from the water displacement.

The annual background mortality rate is estimated from:

$$\Pi_R = 0.51e^{(-3.56xD_W)} \quad (2)$$

with the inclusion of intraspecific variability through a normal distribution with mean equal to D_W and standard deviation equal to D_{Wsd} . Table 3 summarises D_W estimates for the species of interest. A similar approach to growth in terms of accounting for D_W variability is applied here.

Table 3. Mean wood density estimates along with their confidence intervals for each study species.

Species	D_W ($g\ cm^{-3}$)	D_W sd
<i>Abies borisii-regis</i>	0.62	0.04
<i>Abies cephalonica</i>	0.61	0.06
<i>Fagus sylvatica</i>	0.72	0.04
<i>Pinus nigra</i>	0.60	0.05

<i>Quercus frainetto</i>	0.75	0.06
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Simulation Setup and Vulnerability Estimation

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 1.0 m in all study sites. All simulations started from bare ground and lasted for a 1000 year long simulation period. 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°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. In both cases a spin up period of 500 years, where the observed 1950-2013 climate was randomly replicated, was used in order for vegetation to reach an equilibrium with climate. Under the CC scenario during the spin-up period climate was assumed to be similar to BL climate, followed by a transient period of 100 years where temperature and precipitation anomalies were linearly applied until climate stabilizes after year 600.

We performed 30 iterations for each altitude and climate scenario. The key model outputs of interest are a) the annual stand level basal area increment (ΔB) representing an aggregated measure of forest productivity, and b) the absolute (BA_i) and the relative ($r_i=BA_i/BA_T$) contribution species (i) to the stands basal area.

The probabilistic vulnerability algorithm of van Oijen et al. (2013) was subsequently applied to the simulation outputs. In this approach vulnerability is defined as "the expected difference in ecosystem performance between years with and without hazardous conditions". Here we implemented this algorithm to investigate for : a) the vulnerability of stand productivity, expressed by changes in ΔB and b) the vulnerability of community composition, expressed by changes in the relative species contribution to the stands basal area (r_i). Vulnerability (V) is then defined as:

$$V = X_{nh} - X_h \quad (3)$$

where X is the stand level ΔB in the case of forest productivity and r_i in the case of species composition. The nh and h subscripts represent years with non hazardous conditions and hazardous

conditions respectively. Years with hazardous conditions are defined as those for which the annual relative water (ϑ) content is less than the 25% quantile during years with no climate change.

Results

Simulations under current climatic conditions (BL) adequately captured the altitudinal ranges of species distribution across the elevational gradient of the three study sites. At Taygetos, *P. nigra* is dominant at lower elevations with *A. cephalonica* increasing its contribution with altitude (Fig. 2). Following the climate change scenario (CC), the model simulates a strong uphill shift of *P. nigra* across the whole altitudinal gradient and a significant decrease of *A. cephalonica* (Fig. 2). Total stand productivity as expressed here by the annual basal area increment (ΔB) is more vulnerable at lower altitudes (Fig. 5). However community composition is simulated to be more vulnerable at higher altitudes, with *P. nigra* increasing its relative contribution at the expense of *A. cephalonica*

At Pindos South, *Q. frainetto* is more abundant at lower elevation stands (up to 900 m asl) but with increasing altitude *A. borisii-regis* becomes the dominant element of vegetation (Fig. 3) under BL conditions. The applied climate change scenario leads to a significant reduction in the total basal area of the stand at lower altitudes. An uphill shift of *Q. frainetto* is also simulated under CC, leading to a retreat of *A. borisii-regis* (Fig. 4). The vulnerability of stand productivity is stronger at low altitudes (Fig. 6). However simulations suggest that shifts in relative species abundance increases with altitude.

At Pindos North the observed vegetation transition with altitude was simulated under the BL climatic scenario. *P. nigra* dominates the stands up to an elevation of ca 1100 m asl, a mixed forest is simulated between 1150 and 1300 m with *F. sylvatica* dominating the stands at higher altitudes (Fig. 4). At this region, climate change leads to loss of *F. sylvatica* across the simulated gradient. The reduction in total stand productivity is stronger at lower altitudes, with the highest changes in species relative contribution expected at high altitudes (Fig. 7).

All figures are presented at the end of this document.

Discussion

This study presents a framework that integrates field and laboratory work to better parameterise a forest-gap model in order to understand and to project the dynamics of typical forest transitions in Greece. The inclusion of species-specific parameters led to model performance that accurately predicted the standing biomass and the distributional range of expansion of our study species at the

sites of interest. We suggest that vegetation dynamics models, and particularly those that are implemented at local scales should be strongly linked and constrained with site-specific information (Fyllas et al. 2014).

The inclusion of growth and mortality plasticity is an important aspect of this work. Currently there is a great effort to include functional trait variation into models of vegetation dynamics, in order to account for the potential plasticity in the response of ecosystems 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 follow such an approach within existing forest gap-dynamics models, based on the measured intra-specific variability in parameters that control growth and mortality. Under climate change conditions this parameterisation led to simulated declines in species biomass that were more gradual compared to the static parameterisation of the model. This was mainly due to tree growth adjustments and not mortality (results not shown here), as the phylogenetic signal for WD is rather strong with only small variation observed at the species level (Table 3). We only implemented "plasticity" for these two key ecological processes, but other processes could also be considered. For example, including variation in the allometric parameters defining tree architecture could account for potential variation in the competition for light and/or water resources. In any case this variability should be taken into account following an "adaptation" perspective. Practically this means that the distributions of traits/parameters that are inherited by the new recruits (next generation) should be informed by the distribution of mature trees in the stand (previous generation).

Observations of shifts in forest structure and function that could be associated to changes in climatic conditions over the last century have started to accumulate. Changes of tree growth related to temperature increase and/or drought (Jump et al. 2006; Linares and Tiscar 2010), decline in precipitation (Sarris et al. 2011), and/or CO₂ fertilisation (Martinez Vilalta et al. 2008) have been documented for trees established at both low and high altitude sites around the Mediterranean Basin. Increased forest dieback has been attributed to drought (Van Mantgem et al. 2009, reviewed in 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 documented (Allen and Breshears 1998; Penuelas and Boada 2003). Furthermore, some studies report an increase in fire frequency associated with the recent warming, both at 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 in the near future is important in terms of nature conservation and climate change mitigation practices.

Simulation studies have also highlighted the vulnerability of Mediterranean ecosystems to climate change, mainly as an effect of increased drought stress, with forests ecosystems usually projected to shift to shrublands (Schröter et al. 2005; Hickler et al. 2012). At mountainous Mediterranean areas changes in species composition could arise as an integrated effect of drought and fire, with more tolerant species increasing their dominance along altitudinal gradients (Fyllas and Troumbis 2009; Moser et al. 2010). In this study we focused on the effects of drought. In general, our simulations suggest that larger changes in the productivity of mountainous Mediterranean forest are expected at lower altitudes (Figs 5, 6, 7). On the other hand, changes in species composition are stronger at higher altitudes due to the expansion of more drought tolerant taxa under drier conditions and the retreat of less drought tolerant species. However, these shifts can also be species and site specific, depending on both the prevailing climatic conditions and the local species pool. Our results are in agreement with the study of Benito Garzon et al. (2008) where a niche-based model was used to estimate the current and future distribution of some dominant tree species across the Iberian Peninsula. They projected a stronger decrease in the potential distribution of mountainous conifers (less drought tolerant) compared to a lower vulnerability of typical Mediterranean tree species (more drought tolerant). Keenan et al. (2011) combined niche and process based methods to predict the future of forest ecosystems at the same geographic area, suggesting that niche-based methods might overestimate species decline as they do not take into account possible CO₂ fertilisation effects. On the other hand, process-based models that include the potential CO₂ fertilisation effect could overestimate the performance of Mediterranean tree species under global warming conditions, as growth limitation by either water or nutrients availability could also be strong especially in mature forest stands (Korner et al. 2007). In our study CO₂ fertilisation was not taken into account as growth was parameterised using observed tree-ring widths, rather than solving a detailed photosynthesis algorithm. Fire was also not taken into account. Changes in the structure and function of the simulated stands under climate change scenarios were thus mainly mediated through the effects of drought on species growth.

Conclusions

This study presents the use of an integrative framework to explore for the potential effects of climate change on the dynamics of mountainous Mediterranean forests in Greece. Emphasis was

given at incorporating intra-specific variability in growth and mortality. Simulations under climate change conditions suggest an upward shift of more drought tolerant species, a stronger reduction in forest productivity at lower altitudes and significant changes in species composition at higher altitudes. We suggest that the use of field studies designed to cover modelling needs could provide a means to constrain the uncertainty in simulations of forest dynamics, particularly under changing climatic conditions.

Acknowledgments

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Figure 2. Forest Dynamics across the altitudinal gradient of Taygetos under Baseline Climate Conditions (solid lines) and Climate Change Conditions (broken lines).

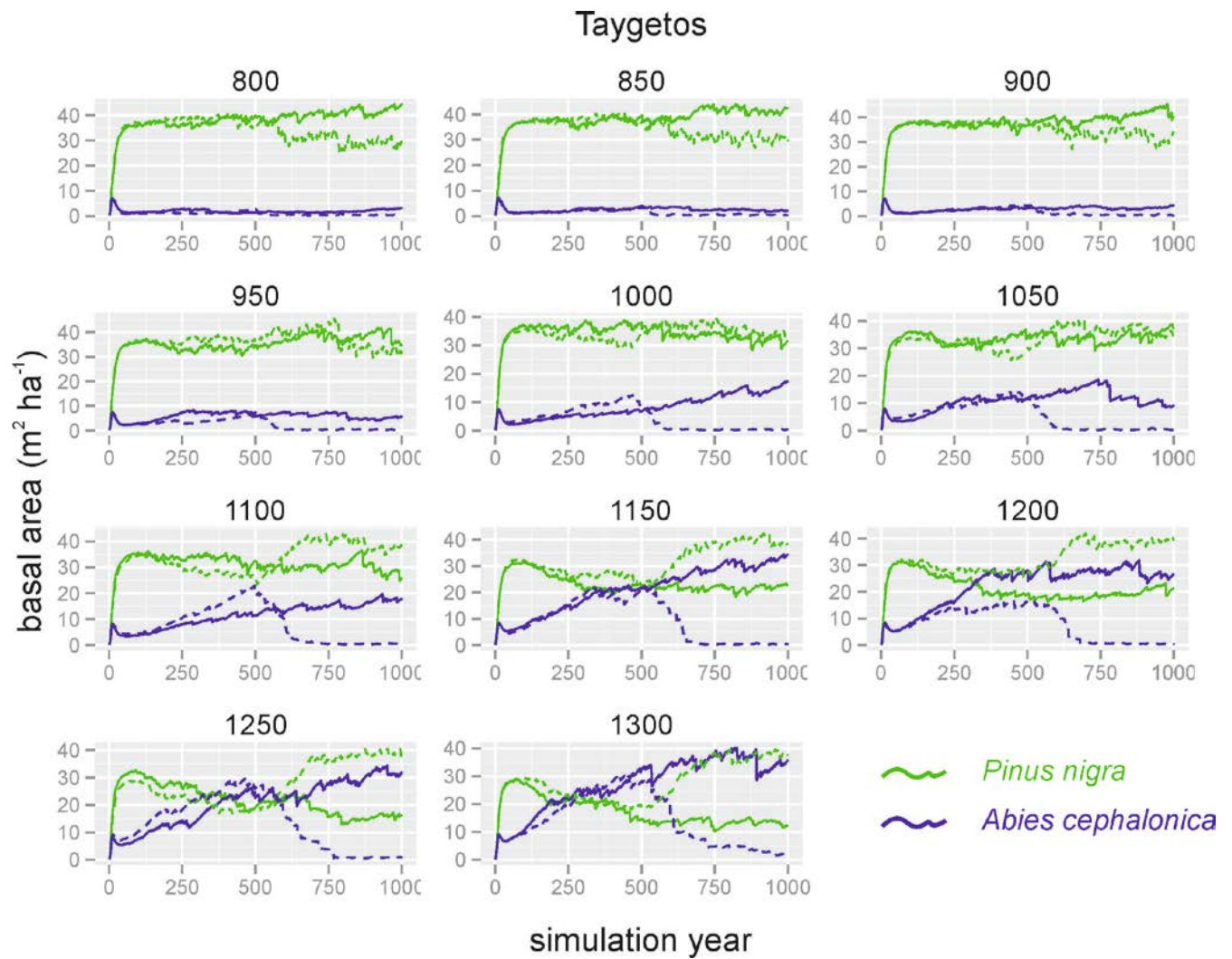


Figure 3. Forest Dynamics across the altitudinal gradient of Pindos South under Baseline Climate Conditions (solid lines) and Climate Change Conditions (broken lines).

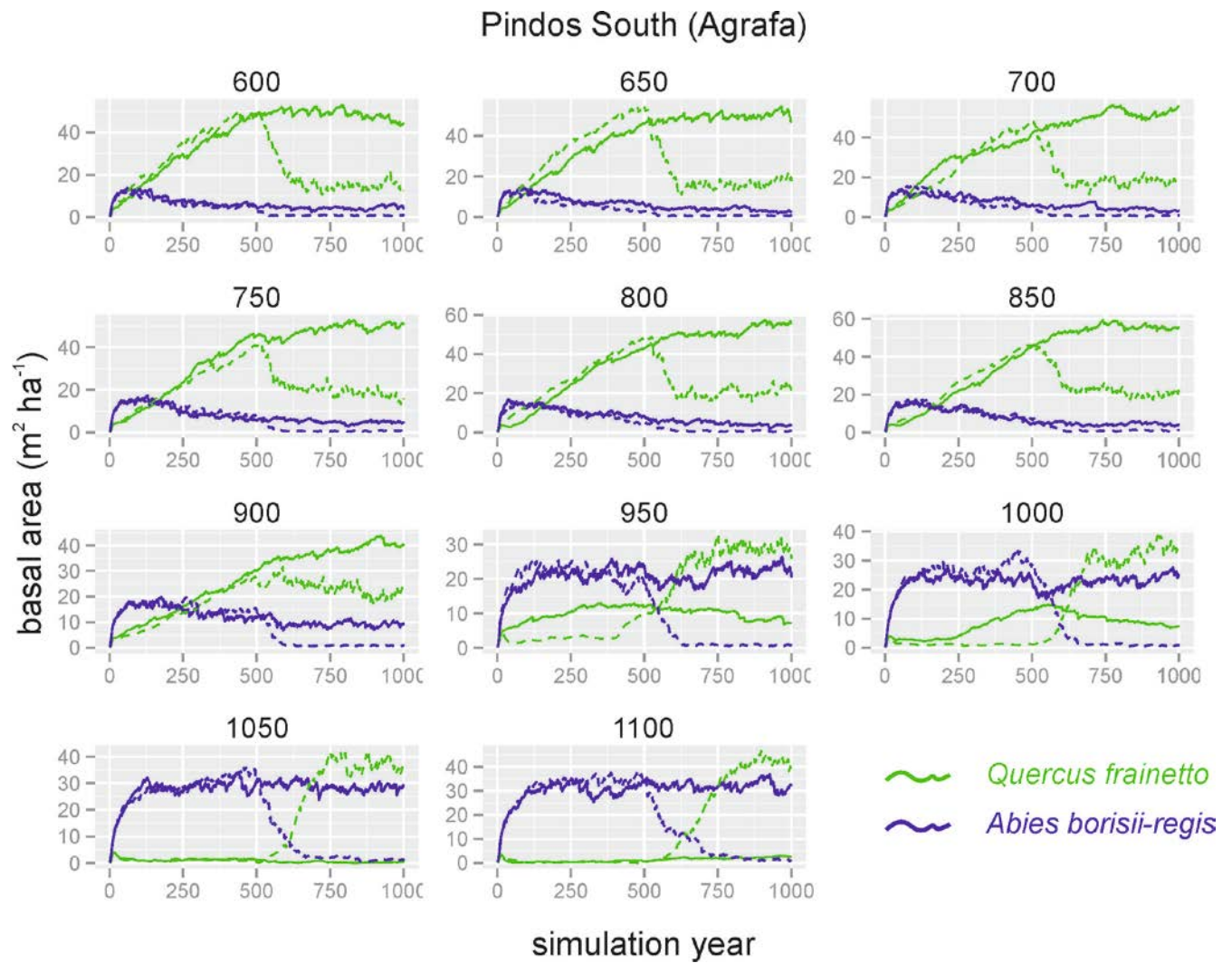


Figure 4. Forest Dynamics across the altitudinal gradient of Pindos North under Baseline Climate Conditions (solid lines) and Climate Change Conditions (broken lines).

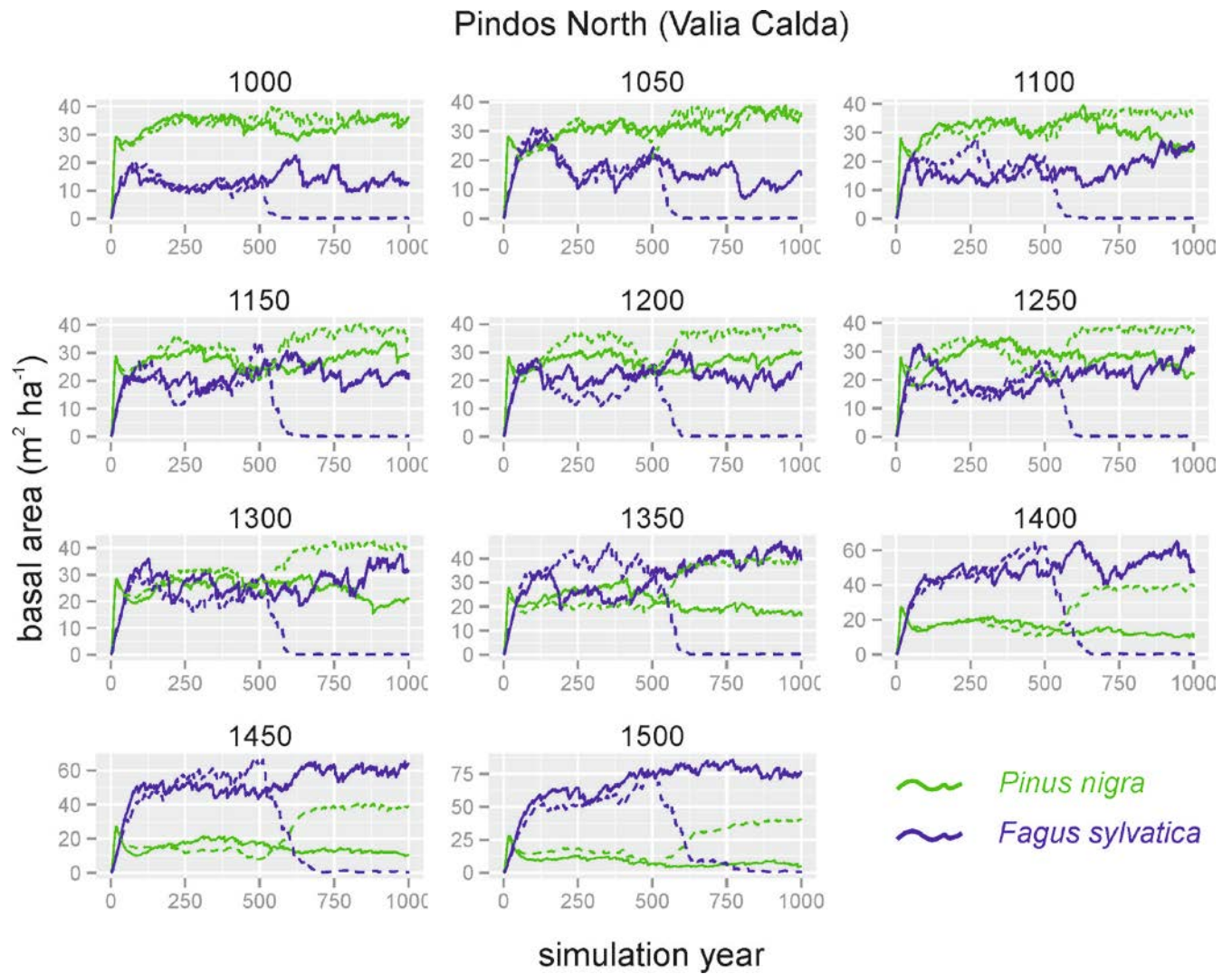


Figure 5. Vulnerability of total stand basal area increment (ΔB) and associated shifts in species relative (r_i) contribution across the altitudinal gradient of Taygetos. See text for details in estimating vulnerability indices.

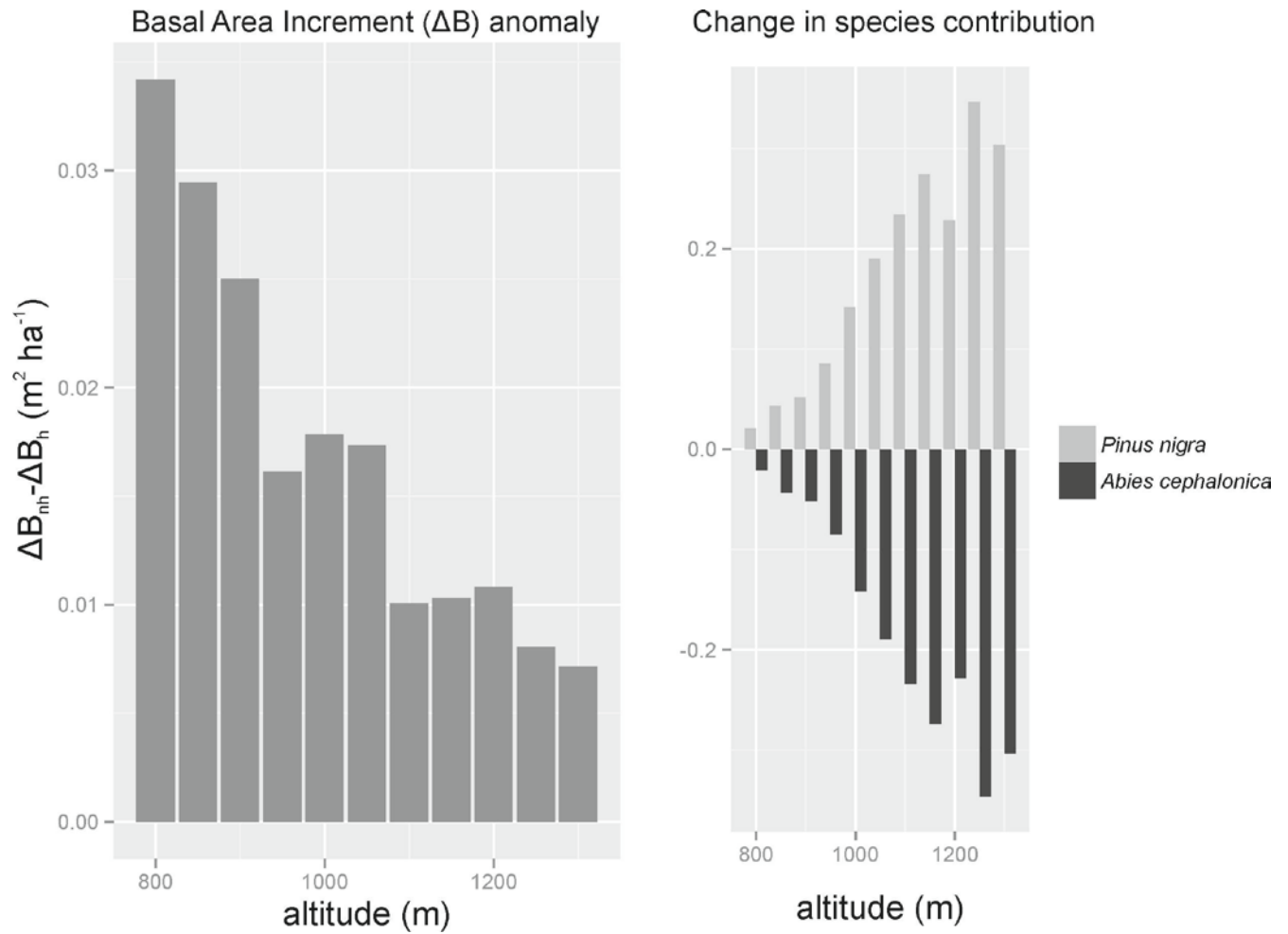


Figure 6. Vulnerability of total stand basal area increment (ΔB) and associated shifts in species relative (r_i) contribution across the altitudinal gradient of Pindos South (Agrafa). See text for details in estimating vulnerability indices.

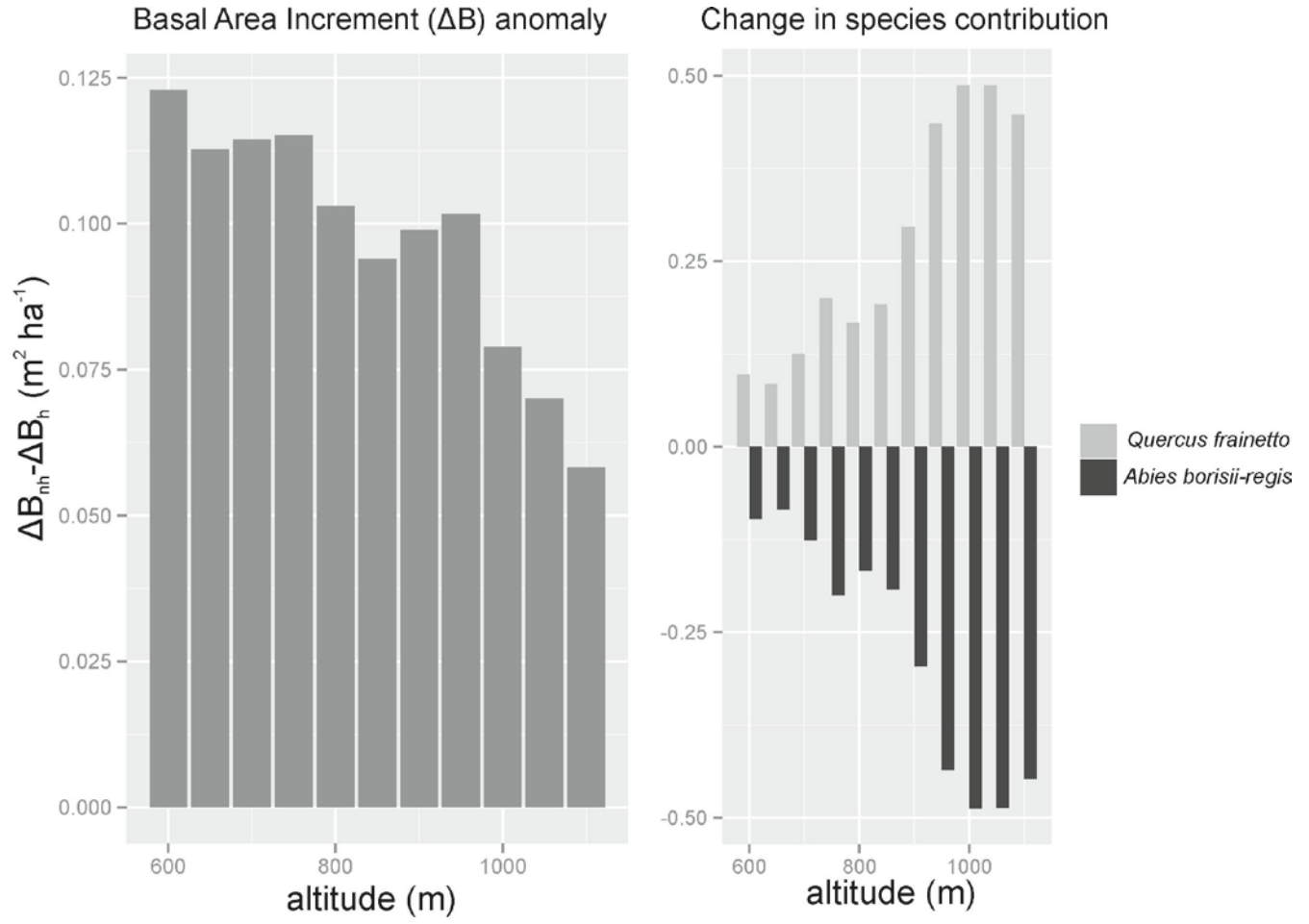


Figure 7: Vulnerability of total stand basal area increment (ΔB) and associated shifts in species relative (r_i) contribution across the altitudinal gradient of Pindos North (Valia Calda). See text for details in estimating vulnerability indices.

