

Geographical adaptation prevails over species-specific determinism in trees' vulnerability to climate change at Mediterranean rear-edge forests

Running head: Adaptation prevails over species determinism

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Abstract

Climate change may reduce forest growth and increase forest mortality rates, which is connected to high carbon costs through reductions in gross primary production and net ecosystem exchange. Yet the spatiotemporal patterns of vulnerability to both short-term extreme events as well as gradual environmental changes are quite uncertain across the species' limits of tolerance to dryness. Such information is fundamental for defining ecologically relevant upper limits of species tolerance to drought and hence, to predict the risk of enhanced forest mortality and shifts in species composition. We investigate here to what extent the impact of short and long-term environmental changes determines vulnerability to climate change of three evergreen conifers (Scots pine, silver fir, Norway spruce) and two deciduous hardwoods (European beech,

sessile oak) at their southernmost limits of distribution in the Mediterranean Basin. Finally, we simulated future forest growth under RCP 2.6 and 8.5 emissions scenarios using a multispecies Generalized Linear Mixed Model. Our analysis provides four key insights into the patterns of species' vulnerability to climate change. First, site climatic marginality was significantly linked to the growth trends: increasing growth was related to less climatically-limited sites. Second, estimated species-specific vulnerability did not match their *a priori* rank in drought-tolerance: Scots pine and beech seem to be the most vulnerable species among those studied despite their contrasting physiologies. Third, adaptation to site conditions prevails over species-specific determinism in forest response to climate change. And fourth, regional differences in forests vulnerability to climate change across the Mediterranean Basin are linked to the influence of summer atmospheric circulation patterns, which are not correctly represented in global climate models. Thus, projections of forest performance should reconsider the traditional classification of tree species in functional types and critically evaluate the fine-scale limitations of the climate data generated by global climate models.

Introduction

Climate change is having a marked effect on biodiversity loss and might further contribute to species range shifts and local extinction as a consequence of ecosystem alteration and desertification expansion (Bellard et al., 2012; Chapin et al., 2000; IPCC, 2014; Thomas et al., 2004). In forests, climate change has already altered species phenology (Menzel & Fabian, 1999; Menzel et al., 2006) and mortality patterns (Allen et al., 2010), directly impacting species composition (Hampe & Petit, 2005) and inducing shifts in species' distribution limits (Chen et al., 2011; Parmesan, 2006; Wilson et al., 2005), sometimes coupled with a net range contraction (Peñuelas et al., 2007; Urli et al., 2014). Climate predictions point to a global increase in temperature and regional changes in rainfall patterns and trends, coupled with a higher frequency of extreme climatic events, leading to an increase of vegetation cover in high latitudes and a decrease in low latitudes and tropical region (Collins et al., 2013; Falloon et al., 2012). Although precipitation is expected to increase globally, the Mediterranean Basin will

likely experience drying due to the rise in temperature and changes in atmospheric circulation patterns (Collins et al., 2013). Specifically, precipitation over the Mediterranean Basin is known to be linked to changes in atmospheric circulation patterns such as the North Atlantic Oscillation (NAO; Fortuny, 2015; Kelley et al., 2012a, 2012b; Vicente-Serrano et al., 2011), which has been demonstrated to influence forest growth in the Mediterranean region (Piovesan & Schirone, 2000; Dorado-Liñán et al., 2017b; Touchan et al., 2017). According to the information provided by instrumental records, the Mediterranean region has already been showing a significant increase in dryness over the last six decades (Hartmann et al. 2013) concurrent with an increase in the frequency of high NAO phases (Bladé et al., 2012; Folland et al., 2009), and drying will likely continue during the next century (Gao & Giorgi, 2008; Ozturk et al., 2015). Such long-term projected changes will presumably lead to an expansion of warmer and dryer climates (Chan & Wu, 2015; Feng & Fu, 2013) as well as to changes in intensity and durations of extreme climatic events (Giorgi & Lionello, 2008; Westra et al., 2014). Those changes could tip into a different vegetation state, but uncertainties of this occurring are still very high (Allen et al., 2010; Bonan, 2008; Lenton et al., 2008).

The increase in the recurrence of drought episodes coupled with the species differences in drought tolerance may destabilize forest ecosystems and induce changes in distribution, dominance and/or species composition (Aitken et al., 2008; Czúcz et al., 2011; Dorado-Liñán et al., 2017a; Gómez-Aparicio et al., 2011; Hanewinkel et al., 2013; Lenoir et al., 2008; Thuiller et al., 2005; Vacchiano & Motta 2015; Zimmermann et al., 2009). Changes in species composition and distribution are expected to influence climate feedbacks by altering albedo, biologically-driven sequestration of carbon from the atmosphere, and the release of greenhouse gases (Pecl et al., 2017).

Moreover, the climate change signal over the Mediterranean region shows significant fine-scale structure due to the complex topography of the region (Gao et al., 2006). Understanding spatial variability in species sensitivity and response to climate, as well as the related drivers, is a fundamental challenge of climate change ecology in order to preserve forest-based biodiversity

and ecosystem services (Clark et al., 2011). Indeed, recent studies have stressed the importance of accounting for geographical variability in population's sensitivity to climate (Matías et al., 2017), as well as explicitly linking vegetation-atmosphere interactions (Dorado-Liñán et al., 2017b) and feedbacks (Zemp et al., 2017). This is considered an efficient way of addressing the vegetation-climate connections still poorly represented in process-based vegetation models.

Tree growth is a good surrogate of tree vitality and performance with a proven potential to provide regionally coherent multispecies growth networks to investigate responses to long-term climate change (Allen et al., 2010; Shestakova et al., 2016; Williams et al., 2013). Differences in tree growth and climate sensitivity are expected across altitudinal and latitudinal gradients according to differences in precipitation and temperature (Jump et al., 2009). Growth responses along altitudinal gradients are generally convergent, with trees displaying an increasing sensitivity to drought with decreasing elevation (Di Filippo et al., 2007; Gea-Izquierdo & Cañellas 2014; Matias et al., 2017). Conversely, studies on latitudinal and longitudinal gradients have been inconclusive, due to the large geographical domain to be covered. In fact, evidence of a higher vulnerability to warm and dry climate at the southernmost limit of a tree species distribution compared to the range core has not been evident (Cavin & Jump, 2016; Hacket-Pain et al., 2016). Furthermore, vulnerability to climate is not even consistent within the rear-edge of different species (Gazol et al., 2015; Dorado-Liñán et al., 2017b; Martínez-Sancho et al., 2018; Sánchez-Salguero et al., 2017; Seim et al., 2014), evidencing that geographically marginal forests are not necessarily climatically marginal (e.g., Tegel et al., 2014).

In this context, the limits of species' tolerance to challenging climate conditions are highly related to the level of conservatism in a plant's hydraulic strategy (i.e., hydraulic safety margins). For example, conifers have theoretically larger hydraulic safety margins and lower sensitivity to vapour pressure deficit (VPD) than broadleaves (i.e., *Fagus sylvatica*) which may counteract their lower ability to repair stem embolisms (Johnson et al., 2012; Carnicer et al., 2013). However, such a distinction is not always clear-cut due to the large differences in ecophysiological behaviour among species within each group (Choat et al., 2012) and

differences within the same species across climatic gradients (e.g., Zang et al., 2014; Frank et al., 2015). Thus, the heterogeneity in the response to climate observed across ecological and geographical gradients may reflect the species' phenotypical plasticity and the ecophysiological strategy of locally adapted populations, which may be as relevant as the differences observed amongst species and plant functional types (Anderegg, 2015; Martinez-Sancho et al., 2017a,b).

This paper addresses a systematic and multispecies analysis aiming at determining what is more influential for species persistence (i.e., tolerance to short- and long-term environmental changes) at rear-edge forests of temperate and boreal species in the Mediterranean Basin: site adaptation or species determinism. The consistent selection and sampling of not only geographically but also climatically limited forests allowed to go beyond the simple collection of sites without a uniform selection criterion. This enabled the identification of site-specific, species-specific, and regional patterns of vulnerability to both long and short-term changes in climate as well as other disturbances. To reach that aim we: (1) determined forests climate sensitivity and tolerance to short term environmental changes (i.e., climate extremes and site disturbances); and (2) assessed their potential vulnerability to forthcoming changes in climate by simulating tree growth of the different temperate and boreal species under different climate scenarios. We additionally (3) tested whether the vulnerability to climate change is not only local but linked to regional climatic patterns and we finally 4) evaluated if the identified regional atmospheric circulation patterns are correctly reproduced by the simulated climate data used for the forests growth projections.

Material and Methods

Site selection, sampling and development of growth chronologies

A field campaign was carried out during summers of 2013 and 2014 across Spain, Italy, Slovenia, Bulgaria and Romania in order to develop a homogeneous and up-to-date tree-ring network of 42 rear-edge forests of five temperate and boreal species comprising conifers and broadleaf tree species (**STable 1**). Specifically, the network was composed of twelve European

155 beech (*Fagus sylvatica* L., beech hereafter), ten silver fir (*Abies alba* Mill., fir hereafter), nine
156 sessile oak (*Quercus petraea* (Matt.) Liebl; sessile oak hereafter), seven Scots pine (*Pinus*
157 *sylvestris* L., Scots pine hereafter) and four Norway spruce (*Picea abies* (L.) H. Karst., spruce
158 hereafter) forests distributed along the southernmost limit of each species current distribution
159 area in southern Europe (**SFig. 1**). The number of sites sampled per species mirrors the
160 limitations to find forests fulfilling all of the following requirements: (i) natural regenerated
161 forests with individuals older than 80 years old, (ii) not heavily managed during the last decades
162 and (iii) where species-specific tree growth is likely limited by high temperature and relatively
163 low precipitation during the growing season, particularly during summer based on the local
164 climatology (i.e., Mediterranean conditions). Concretely, selected sites experienced some sort of
165 summer stress due to either low precipitation, high mean summer temperature or both. There
166 were fewer spruce sites due to the reduced distribution range of this species in southern Europe.
167 Most of the sites were pure stands, or sometimes mixed with other temperate or sub-
168 Mediterranean tree species (e.g., *Quercus pyrenaica* Willd., *Q. pubescens* Willd., *Q. cerris* L.,
169 or *Pinus nigra* Arnold).

170 Generally, beech is considered a shade-tolerant species with a low tolerance to drought and
171 requiring a certain degree of atmospheric humidity to survive (Lendzion & Leuschner, 2008).
172 Sessile oak is assumed to be more resistant to drought than beech (Aranda et al., 2005;
173 Raftoyannis & Radoglou, 2002). Scots pine is a light-demanding species and considered a
174 drought-tolerant conifer (Richardson, 1998), although its strict stomatal control makes it very
175 vulnerable to an early drought-induced growth decline (Martínez-Sancho et al., 2017). Spruce
176 has been described as moderately shade-tolerant and highly vulnerable to drought (Boden et al.,
177 2014; Pretzsch et al., 2014; Zang et al., 2012), even more than beech. According to the
178 literature, spruce and beech would be the least drought-tolerant species and sessile oak and
179 Scots pine the most tolerant ones. Fir is less vulnerable to drought than spruce, but it is unclear
180 whether it is less or more tolerant to drought than beech (Cailleret & Davi, 2011; Zang et al.,

2014). No subspecies or varieties (i.e., *Fagus sylvatica* subsp. *orientalis* (Lipsky) Greuter & Burdet) were included in the sampled forests.

Since the area covered by the study is large, the climate is not homogeneous across sites and a gradient in macroclimatic conditions such as summer temperature and precipitation can be observed in **Fig. 1**: although there are no big differences in summer temperature, the western (Iberian Peninsula) forests generally experienced drier summers than those located in the central (Italian Peninsula and Liguria Gulf) and eastern (Bulgaria and Romania) Mediterranean Basin. Since previous studies revealed geographical differences in tree growth across the Mediterranean Basin (Dorado-Liñán et al., 2017b), such a classification in western, central and eastern sites was used in further analyses.

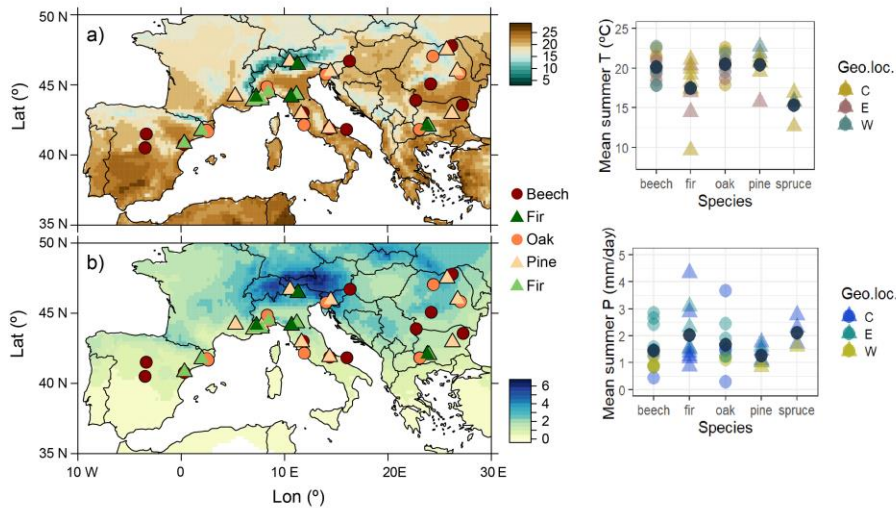


Figure 1. Location and climatology of the 42 rear-edge forests. Circles and triangles correspond to broadleaf deciduous (beech and sessile oak) and conifer forests (fir, Scots pine and spruce), respectively. Species are identified with a colour scale. Symbols are superimposed to the mean summer (June, July and August) temperature in °C (top left panel) and precipitation in mm/day (bottom left panel) for the period 1950-2012 derived from E-OBS. Mean summer temperature (top right panel) and mean daily precipitation (bottom right panel) per site and species are shown with a colour scale according to the geographical

location (*C: central, E: eastern, W: western sites, see methods*). *Black dots correspond to the species' mean value.*

The local climatology of the sampled sites revealed similar summer temperature ranges and means for beech, sessile oak and Scots pine sites (**Fig. 1** and **Table S1** for detailed values). Similarly, differences in mean summer precipitation were not large, although the ranges did differ, with Scots pine occurring under a narrower precipitation range compared to beech and sessile oak (0.8-1.8 mm/day for Scots pine, 0.4-2.8 for beech, and 0.3-3.7 for sessile oak). Spruce sites displayed the coolest mean summer temperature (15.3 °C) followed by fir (17.5 °C), with mean summer precipitation being similar among the two species (2.1 and 2.0 mm/day for spruce and fir, respectively) although the range displayed by spruce (1.6-2.8 mm/day) was narrower than the one of fir (0.9-4.3 mm/day). The coolest summers corresponded to fir and spruce sites growing in central and eastern Mediterranean Basin, whereas the wettest sites correspond to one fir and one sessile oak site located in the central Mediterranean Basin.

The marginality of the sampled sites was characterized by (i) the site climatic marginality index (*Mar*) understood as the distance of a given site to the species niche edge and (ii) the probability that climate change impact exceeds the species niche borders in 2070-2100 (*elmp*) based on 1000 model runs and 63 climate projections following Mellert et al. (2015) (Table S1). *Mar* index is based on climate variables such as temperature of the coldest month and mean temperature and sum of precipitation of the warmest three successive months. Large *Mar* negative values indicate non-marginal position while closer to zero or positive values indicate an outlying niche position (the larger value, the more marginal site is). *Mar* does not distinguish between the rear or leading edge, however, *elmp* indicates the risk of whether climate warming will put a site outside a species niche in future. *elmp* values above 0.5 indicate >50% probability that the climatic conditions at a site will exceed the species niche borders in future. Sites are considered marginal when *Mar* and *elmp* are above -0.5 and 0.5, respectively (Mellert et al., 2015).

In each of the 42 sites sampled, we selected 20 dominant or isolated trees of adult age classes (i.e., older than 80 years except for sites Omic and Pter, where the minimum age was 65) and extracted two cores per tree with an increment borer. Diameter at breast height (DBH) and height were measured for every tree. Samples were visually cross-dated, tree-ring width series were measured using a Lintab measuring table (Rinntech, Heidelberg, Germany) and processed according to standard dendrochronological procedures described in Cook & Kairiukstis (1990). Individual tree-ring width series were converted to Basal Area Increments (BAI) to avoid age-related trends in non-juvenile ring-width measurements (Biondi & Qaadan, 2008). Site chronologies were built by averaging all individual measurements of the same site. The statistical quality of each chronology was checked using the Expressed Population Signal, which is an estimate of the degree to which the set of samples represents the hypothetical perfect chronology. (EPS; Wigley et al., 1984). A threshold value of $EPS > 0.85$ was considered reliable.

Statistical analysis

The common period to all BAI chronologies (1950-2012) was used for further analyses (see **Fig. S2**). Growth trends were characterized per site by the slope of a linear regression between BAI and year for the common period 1950-2012.

In order to quantify the tolerance of each tree species to disturbances (i.e., low-growth periods induced by stressful climatic and/or non-climatic episodes as defined by Lloret et al., 2011), three tolerance indices were calculated at each site: resistance (RT), resilience (RS) and recovery (RC). RT measures the growth reduction induced by disturbances; RS the ability of attaining the same level of growth prior to the negative impact three years after it occurred, and RC the ability to recover from the impact three years after. Negative event years were identified in the individual BAI chronologies at each site following a similar methodology to that used in previous studies (e.g., Cavin & Jump, 2016). Specifically, annual BAI series for each individual tree were transformed into Cropper values and normalized to have a mean of zero and standard deviation of one, prior to extracting the extreme values according to the thresholds described in

Neuwirth et al. (2007). Only negative event years affecting more than 50% of the individual trees were considered for further analyses (see **Table S2**) and consecutive event years were excluded. Three sites did not display negative event years fulfilling those requirements. Tolerance indices to extreme events within three years were calculated per event year following the formulas in Lloret et al. (2011) and a mean value of RT, RS and RC was calculated per species and geographical location. The differences in tolerance to disturbances among species and geographical locations (central, eastern and western sites) were evaluated using the Kruskal-Wallis test and the Nemenyi-test for the pairwise comparisons. A non-parametric test was chosen since the data was not normally distributed in most cases.

To assess the influence of climate on forest growth, a homogenized gridded daily dataset of climate variables over Europe (E-OBS, Haylock et al., 2008) was used as input climate data, due to the lack of station data nearby some of the sampling sites, particularly of Eastern Europe. E-OBS is a publicly available climate dataset at a very high spatial resolution and, although underestimation of some extremes events (particularly precipitation) has been described in areas with low-station density, it reasonably reproduces interannual variations and trends (Hofstra et al., 2009, 2010). Mean monthly temperature and mean daily precipitation were downloaded for the 0.25°x0.25° grid-cell surrounding every sampled site. Seasonal means for precipitation and temperature were calculated as follows: winter (December, January, and February), spring (March, April and May), summer (June, July, and August) and autumn (September, October and November). In order to assess the main climatic drivers of tree growth at regional scales, Principal Component Analysis (PCA) was applied to extract the main modes of variability from the set of site BAI chronologies ($\text{mm}^2 \text{ year}^{-1}$) as well as the seasonal precipitation (mm day^{-1}) and temperature series ($^{\circ}\text{C}$). The association between the scores of the principal components (PCs) extracted from the set of BAI chronologies and the sets of seasonal meteorological variables (precipitation and temperature) was studied using Pearson's correlations. Furthermore, the scores of the principal components were used to assess the relationships between the precipitation and temperature and atmospheric circulation patterns by correlating the PCs with

the sea level pressure field. In this case, we used the seasonal 850mb geopotential height field from NCEP/NCAR (Kalnay et al., 1996). NCEP/NCAR is reanalysis data covering the period 1948 to the present which combines observations and data assimilation.

The Generalized Linear Mixed-Effects Model (GLMM) approach was chosen to fit growth models since our non-independent BAI chronologies dataset better approximated a Gamma distribution (Gea-Izquierdo & Cañellas, 2009). One global GLMM was developed including all five tree species where different combinations of fixed and random factors were tested. As fixed effects we considered climate variables in anomalies (seasons identified as regional drivers of forest growth in the PCA), continuous tree variables such as diameter at breast height and maximum tree height as well as categorical variables such as the tree species. Since the effect of temperature and precipitation on growth might be different for different locations and/or tree species, we tested two random intercepts aiming at characterizing idiosyncratic variation in site response to climate linked to (i) geographical position (using the values of longitude for the 42 sites) and (ii) tree species. Starting from a saturated GLMM model, we created the fully crossed set of models including the different random and fixed effects and considering interactions among variables. Model selection was conducted based on ANOVA including AIC (Akaike Information Criterion) with lower AIC values indicating a model's higher explanatory power. The significant contribution of the random effects included in the selected GLMM was confirmed using Likelihood Ratio Tests. Collinearity among predictors was checked by the Kappa criterion and the Variance Inflation Factor (VIF; Zuur et al., 2010). The predictive skills of the selected model were evaluated by the leave-one-out cross-validation and model quality was checked by inspecting residual patterns and looking for signals of heteroscedasticity (Zuur et al., 2009).

The selected multispecies GLMM was used to estimate growth at the 42 sites under contrasting climate change scenarios. For the forest-growth projections run along the 21st century (i.e., 2013-2100), we used the temperature and precipitation output of global climate model (GCMs) simulations generated by the Coupled Model Intercomparison Project Phase 5, included in the

last Intergovernmental Panel on Climate Change report (IPCC, 2014). Two contrasting representative CO₂ concentration pathways (RCP; van Vuuren et al., 2011) were considered: the *mitigation* scenario RCP2.6, in which the concentration of CO₂ reaches its maximum before 2050 and then declines, aiming at keeping temperatures likely below 2°C above pre-industrial levels; and the RCP8.5, that considers a high emissions scenario with CO₂ concentrations linearly increasing till 2100 and projections of an increase in global temperatures between 2.6 and 4.8 °C in 2100. The mean of 32 and 29 global climate models was used in the RCP2.6 and RCP8.5, respectively.

These GCMs simulations were used to 1) test the skills of the GCMs in reproducing the fine-scale climate variations in the Mediterranean Basin during the calibration period 1950-2012 by comparing simulated and instrumental climate patterns; and 2) as input climate data for the 2013-2100 forest-growth projections using the developed GLMM.

All analyses were done using R software version 3.2.3 (R Core Team, 2015) and packages dplR (Bunn, 2008), psych (Revelle, 2017), forecast (Hyndman & Khandakar, 2008), PMCMR (Pohlert, 2014), lme4 (Bates & Maechler, 2009), MASS (Venables & Ripley, 2002), MuMIn (Bartoń, 2011), and mlmRev (Bates et al., 2014).

Results

Tree growth and climatic marginality

Marginality indices evidenced that most of the sites sampled are not only geographically marginal (**Fig. S1**), but also climatically marginal (**Fig. 2 and Table S1**). According to *Mar*, 27 out of 42 stands are outside the species niche borders or situated close to the niche edge (*Mar* > -0.5), 11 sites are in intermediate niche positions (*Mar* between -2 and -0.5) and only 4 sites are in central niche position (*Mar* < -2). However, only two forests (one fir and oak forest) displayed *elmp* values below 0.5, denoting that climatic conditions at 40 out of the 42 forests under study will likely exceed the species' tolerance limit in future. The probability of exceeding the species niche borders in future is asymptotically linked to the current climatic marginality of the site

(**Fig. S3**) a *Mar* value above -1 triggers the chances of exceeding the species' tolerance limit in future to more than 80%. Furthermore, the climatic marginality of the site was significantly linked ($p < 0.05$) to the slope of the growth trend: increasing growth was related to lower site marginality (**Fig. 2b**), whereas no significant relationship was found with *elmp* (**Fig. 2c**).

Most of the populations showing significant increasing growth in the centre of the Mediterranean Basin are high-elevation conifers growing in the alpine region (north of the Italian Peninsula) under moister and/or cooler climate (**Fig. 2a; Table S1**). Similarly, the broadleaf deciduous forests displaying significant increasing growth were low-elevation forests in eastern Mediterranean, mainly of sessile oak, growing under more favourable climate conditions. Generally, beech and medium-elevation conifers such as Scots pine displayed the lowest amount of significant increasing trends and even severe growth reductions at some sites, particularly for Scots pine. This is in line with the higher proportion of climatically marginal sites for Scots pine (6 out of 7; **Table 1**). Conversely, the largest growth increase corresponded mainly to sessile oak, fir and spruce forests (**Fig. 2a; Table 1**), which are the species displaying a higher proportion of sites on intermediate and central niche positions. Despite this, we could not find a clear link between growth trend and summer climate variables or elevation (See **SFig. 4**)

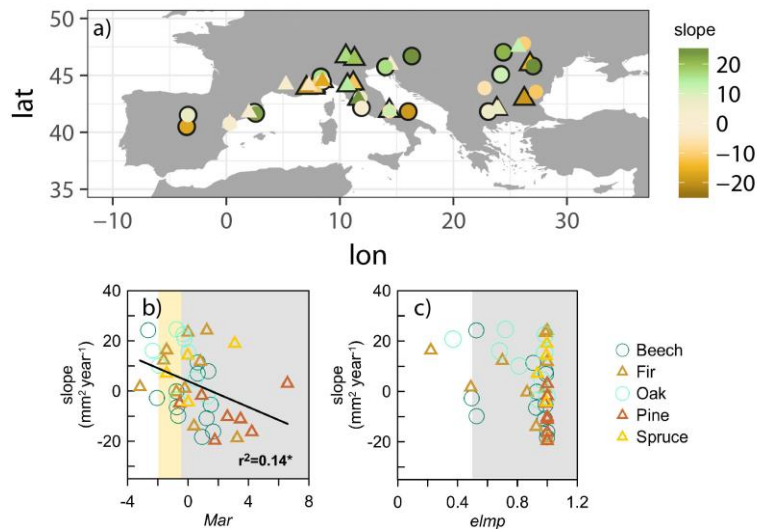


Figure 2. Growth trends for the period 1950-2012. a) Map displaying sign and significance of the growth trend ($\text{mm}^2\text{year}^{-1}$) estimated as the slope of a linear regression between basal area increment and year for the period 1950-2012. Triangles and circles correspond to conifer and broadleaf deciduous forests, respectively. Symbols with a black outline correspond to a significant trend ($p < 0.05$). Bottom graphs show the relationship between growth trend and b) climatic marginality index *Mar* and c) probability of exceeding the species tolerance limits in 2070-2100, *elmp*. Grey and yellow-shaded areas highlight marginal and intermediate niche position, respectively (Mellert et al., 2015). (*) indicates significance at 0.05

Species tolerance to disturbances

Rear-edge fir and Scots pine populations appeared as the most resistant to disturbances followed by those of sessile oak, being beech the least resistant species and displaying a significantly lower resistance capacity than fir (**Fig. 3 and STable 3**). However, no significant differences were found in the resilience capacity among species. Beech showed the largest recovery capacity within three years, whereas Scots pine displayed a significantly lower recovery capacity compared to beech.

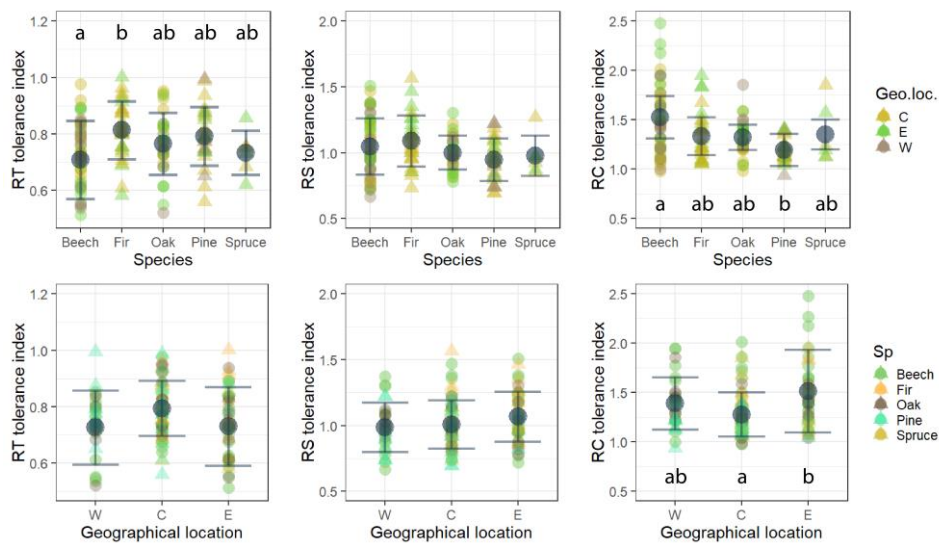


Figure 3. Individual values, mean and standard deviation of tolerance indices resistance (RT), resilience (RS) and recovery (RC) per species (upper panels) and geographical position

(lower panels). Color indicates geographical position and tree species in the upper and lower panels, respectively. Different letters indicate significant differences ($p < 0.01$) among groups according to the Kruskal-Wallis test and post-hoc Nemenyi-test for pairwise-comparison.

We also observed some geographical differences in RT, RS and RC according to the forest geographical location in the Mediterranean Basin (**Fig. 3**), however only the difference in the recovery capacity between central and eastern populations was significant ($p < 0.01$). Central populations were slightly more resistant to disturbances (although the difference respect to western and eastern populations was non-significant) at the expense of a significantly diminished recovery capacity compared to eastern populations.

Modelling forest growth for the multi-species network

The PCA run with the 42 BAI chronologies revealed that the first three PCs explain 49% of the total tree growth variability (22%, 17% and 10%, respectively) and evidenced that spring and particularly summer climate were the main drivers of tree growth at regional scale (**Figure 4**).

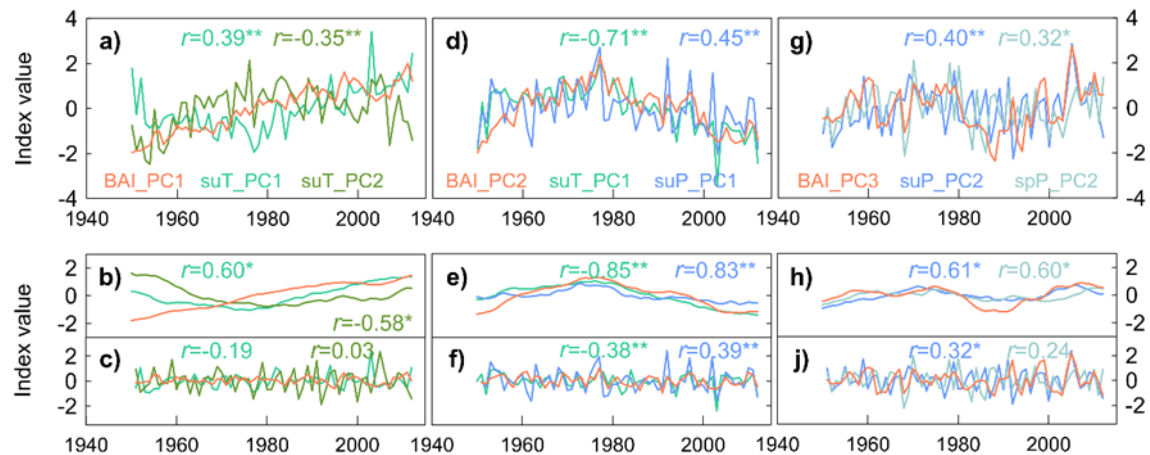


Figure 4. Correlations of the first, second and third tree growth PC scores (left, middle and right panel, respectively) with the PC scores derived from the analysis with spring and summer temperature and precipitation. Upper panels (a, d, g) display the full-time series and the corresponding correlations. Middle (b, e, h) and lower (c, f, j) panels display low and high-pass filtered series and the corresponding correlation values, respectively. Series are

*filtered with a centered 10-years moving average. suT: summer temperature; suP: summer precipitation; spP: spring precipitation. suT_PC1 in the middle panel is inverted for a better visualization. * and ** indicate significance at $p<0.05$ and $p<0.01$, respectively.*

The correlation between the scores (time series) of PCs derived from the observed seasonal temperature and precipitation records and the BAI chronologies disclosed significant relationships between BAI and summer temperature (**Fig. 4a-c**) and summer and spring precipitation records (**Fig 4d-f** and **4g-j**) on different frequency domains. Correlations of growth PCs with temperature PCs are generally negative whereas with precipitation PCs are positive, denoting opposite influences of climate variables on tree growth. Except for correlations between the PC1 of BAI and the first two PCs derived from summer temperature (**Fig. 4a-c**), the relationships among variables are steady across different frequency domains (i.e., correlation with low- and high-pass filtered series), evidencing consistent climatic influence on interannual and long-term tree growth.

The result of the PCA identified summer temperature and precipitation as the most relevant climate predictors of forest growth. The comparison among different GLMM with different combinations of fixed effects (summer temperature and precipitation, spring temperature and precipitation, DBH, height and tree species) and random effects, revealed that the model considering DBH and spring and summer climate as predictors and accounting for the variation in site responses to climate linked to geographical position, displayed the lowest AIC value. The same model with the interaction species and climate as fixed effects or accounting for the variation in site responses to climate linked to tree species, displayed higher AIC values (see **STable 4**). Even when considering partial random effects, (i.e., variation in response to summer precipitation or summer temperature separately), the random effect species-climate always displayed higher AIC than the random effect site-climate (**STable 5**).

The results of the selected global GLMM disclosed that tree growth (BAI) at the study sites depended on the size of trees (as estimated by DBH) and was mainly controlled by summer temperature and precipitation and, to a lesser extent, by spring temperature and precipitation

(**Table 1**). Standard tests revealed negligible collinearity among predictors (VIF=1.03; Kappa=7.6) and non-overdispersed data. By-site random effect of suT and suP (**STable 6**) explained 12% of the total variance explained by the model. The relatively lower amount of variance explained by random effects occurred because most variation due to suT and suP was already explained by the fixed effects (88%). Despite this, the contribution of the random effects to the GLMM was highly significant ($p<0.0001$).

<i>Fixed effects</i>	Estimate	Std. Error	t-value	p-value
<i>suT</i>	-80.659	9.874	-8.19	< 0.001
<i>suP</i>	96.026	7.687	12.49	< 0.001
<i>spP</i>	34.767	6.183	5.62	< 0.001
<i>spT</i>	23.906	6.672	3.58	<0.001
<i>DBH</i>	43.885	1.901	23.09	<0.001

Table 1. Parameters for fixed effects in the selected generalized linear mixed effects model (GLMM) using BAI ($\text{mm}^2 \text{ year}^{-1}$) of the 42 sampled sites as dependent variable for the period 1950-2012. The influence of other tested fixed and random parameters can be found in Stable 4. suT: summer temperature; suP: summer precipitation; spP: spring temperature; spT: spring temperature; DBH: diameter at the breast height. Values for the random effects can be found in Table S6.

The negative effect of summer temperature (suT), revealed the general reverse effect of suT on tree growth ($p<0.001$). Conversely, summer and spring precipitation (suP and spP, respectively) displayed a positive effect ($p<0.001$) as well as spring temperature (spT). Other allometric variables such as mean tree height or categorical variables such as tree species did not significantly improve the model (**STable 4**). Thus, tree growth was mainly impaired by summer climate and growth rates were related to tree size (i.e., larger trees displayed higher growth rates) but independent of tree species within our network. The coefficient of by-site effect of suT revealed that summer temperature had a different influence depending on the site, whereas the by-site effect of suP showed a homogeneous positive effect across sites (**STable 7**). This is

connected to the local climatology: sites with lower mean suT usually displayed positive coefficients, whereas all sites showed positive coefficients for suP regardless of the local amount of summer rainfall (**SFig. 5**).

Projections of forest growth under different emission scenarios

The predictive skill of the selected model ($r=0.83$; $R^2_{\text{pred}}=0.70$) pointed to an overall good model performance with no significant differences in the predictive ability across species and geographical location (**SFig. 6**).

Projections under the *mitigation scenario* RCP 2.6 mostly revealed non-significant growth trends from 2013 to 2100, with few exceptions (**Fig. 5**). Among the significant growth trends, increasing growth was detected in conifer species (i.e., fir and spruce) located at mountain areas in the centre of the Mediterranean Basin, in the Italian Peninsula, although few broadleaf forests in the centre and eastern of the Basin also displayed increasing growth trends. This seems to be connected to forest vitality since forests displaying increasing growth under RCP2.6 usually showed increasing growth during the period 1982-2012 and lower *Mar* values (**SFig. 7**). Similarly, significant growth reductions were only projected for some beech and Scots pine forests in line with the decreasing growth trend usually displayed by these forests and linked to a larger proportion of marginal sites, particularly for Scots pine. Conversely, growth projections under the *high emissions scenario* RCP8.5 revealed a generalized significant growth reduction across the Mediterranean Basin by 2100, regardless of the species and geographical location, being the growth reduction particularly severe in the eastern Mediterranean. Still, few significant increasing growth trends were projected for some fir forests located in the central Mediterranean Basin.

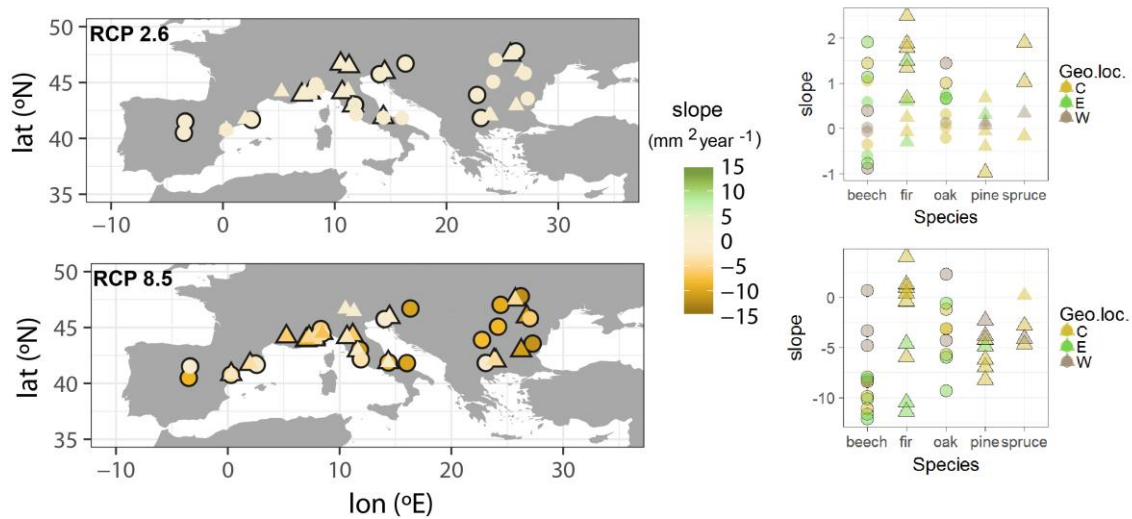


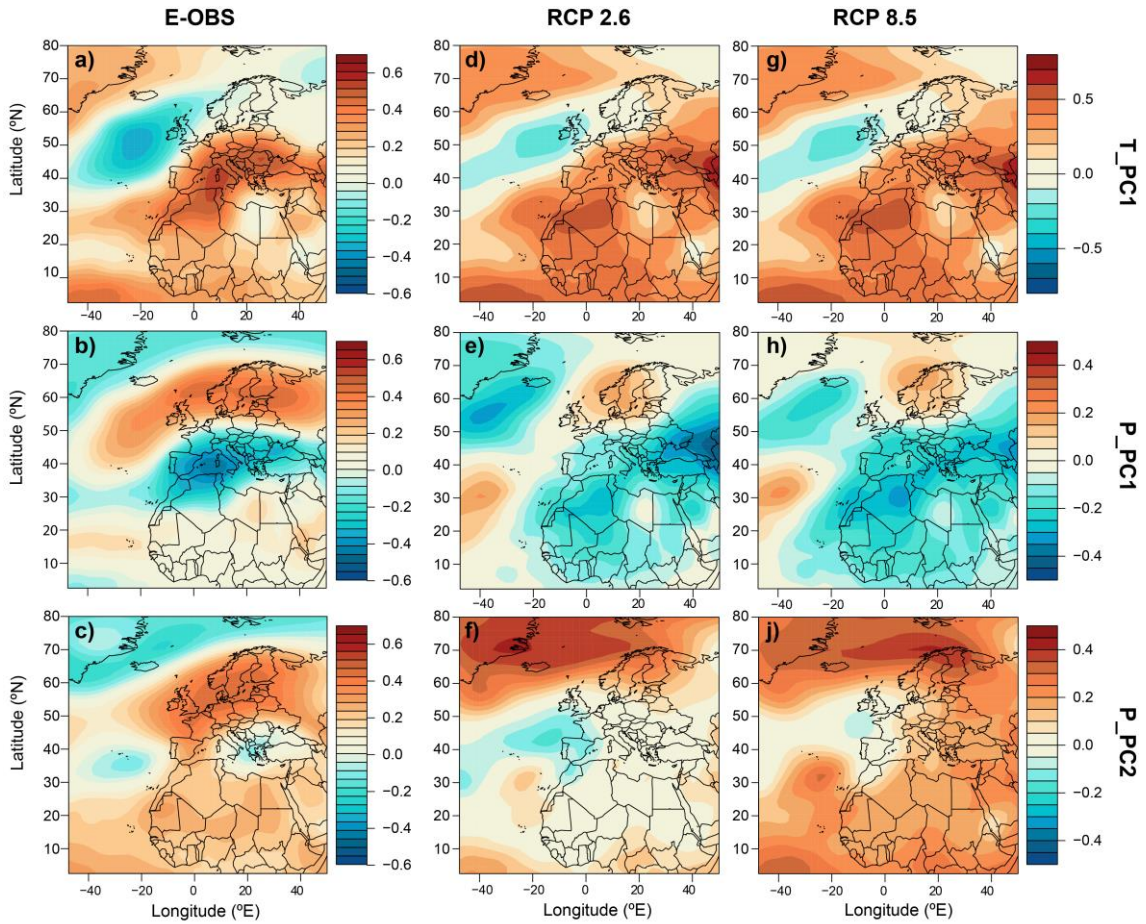
Figure 5. Projected growth trends between 2012 and 2100 under the RCP2.6 (upper panel) and RCP8.5 (lower panel) scenarios. Growth trends were estimated as the slopes of the linear regressions between basal area increment and year. Right panels display the slope of the growth trends per species. Triangles and circles correspond to conifer and broadleaf deciduous forests, respectively. Symbols with a black line correspond to significant trends ($p < 0.05$).

Broad-scale drivers of forest growth: teleconnections

The PCA revealed geographical patterns of tree growth across the Mediterranean Basin, being particularly relevant the east-west polarity encapsulated in PC3 with neutral to positive correlations in the eastern Mediterranean and neutral to negative correlation in central and western Mediterranean. (**SFig. 8**). The analysis of the relationship between the PC scores derived from climate variables and the field of geopotential height, helped elucidating whether those geographical patterns of tree growth are related to atmospheric circulation patterns as described in previous studies (e.g., Chen et al., 2015; Dorado-Liñán et al., 2017b; Seim et al.,

2014). The correlation between PC1 derived from the summer temperature and summer precipitation and the field of 850mb geopotential height revealed similar atmospheric circulation patterns (**Fig. 6 a,b**). The mode of cyclonic circulation described by the two patterns was centred over the Ligurian Sea, close to the French and Italian coasts, and a second centre over the eastern Mediterranean. This pattern was linked to higher precipitation and lower temperatures in the centre of action and decreasing influence towards the western Mediterranean Basin. The correlation between the geopotential height pattern and PC2 related to summer precipitation (**Fig. 6c**) represented cyclonic circulation centred in the eastern half of the Basin and linked to higher summer precipitation and lower summer temperatures in this region.

Concerning simulated summer climate data by GCMs, the synoptical patterns described by the simulated temperature data for the period 1950-2012 under RCP 2.6 and RCP 8.5 (**Fig. 6d, g**, respectively) depicted some similarities with the observational pattern (**Fig. 6a**). Conversely, the pattern described by the simulated precipitation data considerably differed from that described by the observational data: the PC1 of simulated summer precipitation displayed a centre of action displaced towards the east (**Fig. 6e, h**, for RCP 2.6 and 8.5, respectively), whereas the PC2 did not show the east-west polarity across the Mediterranean Basin depicted by the PC2 of the E-OBS data (**Fig. 6f, j**, for RCP 2.6 and 8.5, respectively). The differences in the dynamical patterns between observed and modelled climate translated into different temperature and precipitation distribution patterns across the Mediterranean Basin (**Fig. 7**).



496

497 *Figure 6. Spatial patterns of correlations of PCs derived from observational and simulated*
 498 *climate data with the field of summer 850mb geopotential height (NCEP/NCAR) for the*
 499 *period 1950-2012. Correlation field of the first PC derived from E-OBS observational*
 500 *summer temperature (a) and first and second PCs derived from observational summer*
 501 *precipitation data (b, c, respectively). The corresponding spatial patterns for simulated*
 502 *summer temperature and precipitation data are given for emission scenarios RCP 2.6 (d, e, f,*
 503 *respectively) and RCP 8.5 (g, h, j, respectively).*

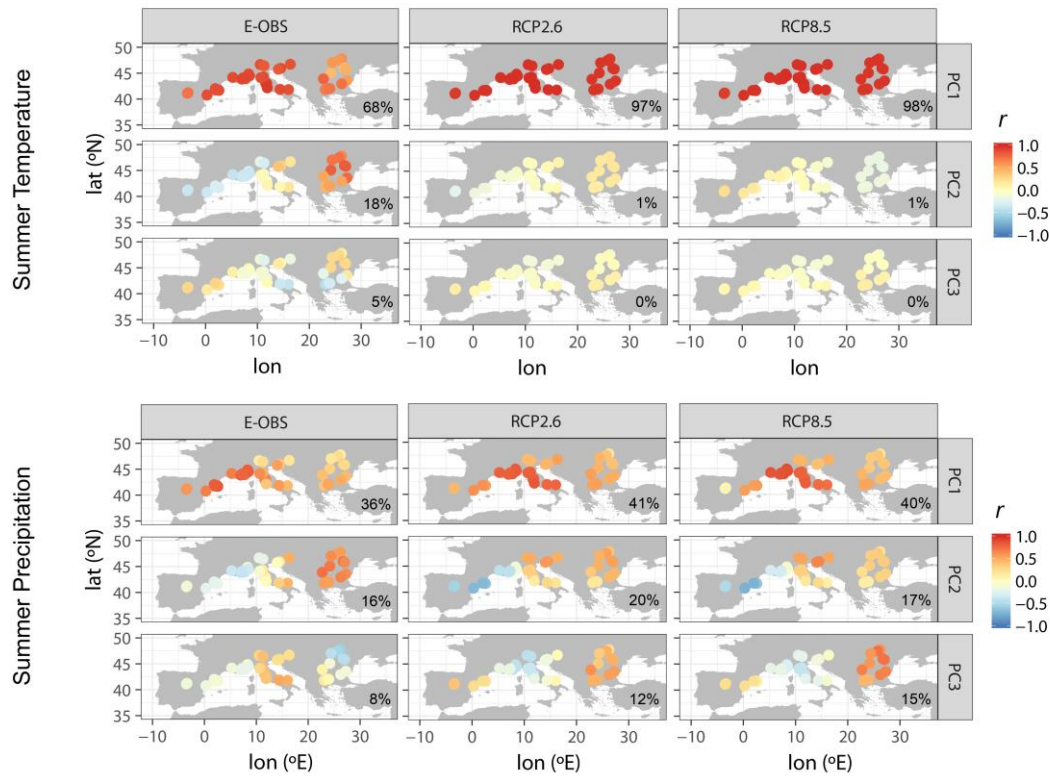


Figure 7. Spatial patterns of observed and simulated summer climate data. Upper panel displays the correlations of the individual summer temperature series with the first, second and third PC (upper, middle and lower map, respectively) using observational (E-OBS) and modelled (RCP2.6 and RCP8.5) climate data for the period 1950–2012. Bottom panels display the same analysis for summer precipitation. The percentage of explained variance by each component is shown in the corresponding map.

The observed mean summer temperature data (i.e., E-OBS) showed geographical differences across the Mediterranean Basin not reproduced by the simulated temperature data under RCP 2.6 and 8.5 scenarios (**Fig. 7**). Furthermore, 97% and 98% of summer temperature variability is confined in PC1 in simulations under RCP2.6 and RCP8.5, respectively, whereas the observational data displayed a 68% of summer temperature variability explained by PC1 and larger contributions of PC2 and PC3 (18% and 5% of variability, respectively). Conversely, summer precipitation displayed similar contributions in variability of observational and simulated climate data and similar geographical patterns for PC1 and PC2. The only relevant

difference was observed in the geographical pattern of PC3, in which simulated summer precipitation under RCP 2.6 and 8.5 scenarios described a different gradient across the Mediterranean Basin to that showed by the observation data.

Discussion

Summer climate constrains tree growth across species and sites at the rear-edge

Rear-edge beech and Scots pine forests displayed a higher proportion of declining growth trends than the rest of species. However, we also found some forests displaying significant increasing growth trends during the last decades, which is not unprecedented at the rear edge (Di Filippo et al., 2007; Galván et al., 2014; Gazol et al., 2015; Matías et al., 2017). In our particular case, most of the positive growth trends were located in the centre and east of the Mediterranean Basin and linked to sites under cooler and moister climate conditions and lower marginality indices (i.e., less-climatically marginal). It should also be taken into consideration that current low-altitudinal limits of species' distribution might be located above the natural altitudinal limits (i.e., cooler temperature and higher precipitation) and therefore, less climatically constrained since past land use and silvicultural activities have altered natural species distribution (Colombaroli et al., 2013; Tilman & Lehman, 2001; Silva et al., 2012). Indeed, historical changes in forests' distribution and composition in central Italy were strongly driven by human socio-political decisions, having severe impacts on meso-hygrophilous forest types (Mensing et al., 2018; Piovesan et al., 2018). Thus, *a priori* geographically marginal populations might not be climatically marginal, as demonstrated by the marginality index *Mar*, due to either particularities on local climatology and/or alteration of the species' natural distribution limits. In this sense, *Mar*, has proven to be a better indicator explaining growth trends than summer climate variables, most likely because it integrates a more complete climate picture and considers different warm seasons for different sites.

Despite the presence of positive growth trends, our results show that tree growth of temperate and boreal species at the rear-edge in the Mediterranean Basin has generally not increased in

recent decades and growth trends are not only linked to climate. Indeed, the comparison of time series derived from PCA, revealed that long-term growth trends confined in PC1 might not only be a function of climate, but could also be the result of additional global or local factors such as CO₂ fertilization, nitrogen deposition, and changes in forest structure (Zhu et al., 2016).

Previous studies reporting broad-scale declining growth patterns in the peri-Mediterranean region usually describe a generalized positive influence of summer precipitation on tree growth and a less homogeneous negative influence of summer temperature, pointing to generalized seasonal water limitation (e.g., Cavin & Jump 2016; Dorado-Liñán et al., 2017b; Gazol et al., 2015; Hacket-Pain et al., 2016; Jung et al., 2017; Matias et al., 2017; Sánchez-Salguero et al., 2015). We also found a more generalized positive effect of summer precipitation than negative effects of summer temperature across sites. Few forests (mainly conifer forests) did not show a negative influence of summer temperature on growth, most likely because they were not as climatically restricted as other rear-edge forests (Gazol et al., 2015; Seim et al., 2014). In fact, and according to the local climate conditions, fir and spruce sites were on average cooler than those of beech, sessile oak and Scots pine.

Several studies have described a determinant influence of winter and early spring temperatures on distribution and growth of both conifers (Gea-Izquierdo et al., 2015; Matías et al., 2017; Sanchez-Salguero et al., 2015) and broadleaf deciduous species (Gea-Izquierdo & Cañellas, 2014; Vitasse et al., 2011; 2014) close to the rear-edge. We did find a significant influence of spring climate on growth in our multispecies forests network. However, winter temperature was not a relevant variable in our model, likely because the risk of freezing damage usually associated to low temperatures during the cold season (Larcher, 2005) was not generalized across the rear-edge forests under study.

The role of disturbances: resistance-recovery trade-off

All species displayed comparable resilience capacity (i.e., no significant statistical differences were found among species) and, although most of pair-comparisons revealed non-significant

differences, fir displayed a higher resilience and resistance capacity than the rest of species, in agreement with previous studies (Elling et al., 2009; Vitali et al., 2017; Zang et al., 2014). Some recent studies pointed out that functional diversity in fir forests may mitigate the negative effects of extreme droughts (Gazol & Camarero, 2016) while others reported that growth reductions in rear-edge conifers forests are more linked to site characteristics (climate and density, e.g. basal area) than tree species (Serra-Maluquer et al., 2018). Notably, fir and spruce sites were on average cooler and wetter during summer than beech, sessile oak and Scots pine sites, and these more favourable conditions during summer could have buffered the vulnerability of those forests to climate-induced disturbances. Due to the selected experimental design, genetically isolated populations such as those of fir from Southern Italy and the Pyrenees were not considered in the present study. Including these or other genetically isolated populations would help to further understand species-specific responses to climatic extremes in future analyses.

The few significant species-specific differences in tolerance indices found evidenced a trade-off between resistance and recovery capacity, as hypothesised by Lloret et al. (2011), and later reported in studies analysing growth resilience across Northern Hemisphere forests (Gazol et al. 2017). Indeed, different tolerance patterns among species have been described across regions and biomes (Gazol et al., 2017, 2018). In our study, beech forests displayed a significantly lower resistance but the highest recovery capacity, consistent with leaf physiological studies (Pflug et al., 2018); whereas Scots pine showed a resistance capacity almost as high as that of fir at the expense of a significantly lower recovery capacity. Such a persistence-productivity trade-off has been described by similar studies at the species range core as well as at the rear edge (Cavin & Jump, 2016; Galiano et al., 2011; Martínez-Vilalta et al., 2012; Zang et al., 2014). At the tree physiological level, trade-offs are caused by allocation of limited resources to one purpose vs. another (Reich, 2014), though the underlying mechanisms are difficult to disentangle. In the specific case of beech, the reduction of growth at an early stage of a disturbance (i.e., drought) could be either due to a strategical stomatal closure to avoid damages

(e.g., Aranda et al., 2005), to massive mast seeding that usually synchronizes with drought events in this species (Hacket-Pain et al., 2015; Piovesan & Adams, 2001; Vacchiano et al., 2017) or a combination of both. Conversely, the low recovery capacity of Scots pine could be hypothetically either due to a strict stomatal control that reduces the carbon reserves available for recovery, or to the repair costs of embolisms as a consequence of keeping high stomatal conductance under unfavourable conditions (Adams et al., 2017). These two strategies are opposite, however the coexistence of contradictory ecophysiological strategies within the same species is not unprecedented: differences in ecophysiological behaviour, xylem adaptation and tolerance indices across regional scales have been described for the same species or species belonging to the same functional group (e.g., Frank et al., 2015; Martínez-Sancho et al., 2017; Zang et al., 2014). For instances, beech is usually described as an anisohydric species under a genuine temperate climate (Pretzsch et al., 2013) but displays a typical isohydric behaviour under drier conditions at the southernmost edges of the species distribution (Aranda et al., 2000, 2005). Spruce was not found to be as vulnerable to drought and disturbances as described in previous studies in the core distribution range (Pretzsch et al., 2013; Zang et al., 2012), maybe due to a certain ability to adapt along climatic gradients (Zang et al., 2014). The same reason could apply to fir, which appeared to be more resistant to drought than beech at the core range (Zang et al., 2014) but not at the range edge in the Mediterranean Basin (Cailleret & Davi, 2011). Therefore, it seems more realistic to consider the hydraulic strategy as a function of ecotype or acclimation rather than a species-wise determinism. Because of this, the categorical classification on anisohydric/isohydric species is being debated lately (Klein, 2014; Martínez-Vilalta & Garcia-Forner, 2017) and the arrangement of tree species in fixed functional types for modelling exercises has been questioned (Anderegg, 2015).

The described species resistance-recovery trade-off is further underpinned by the higher resistance of central Mediterranean populations linked to a significantly lower recovery capacity than that of forests located in the eastern Mediterranean. At the central Mediterranean Basin several sites are located close to the alpine area (north of the Italian Peninsula) where forests

grow under a milder climate. As previously hypothesised by Martínez-Vilalta et al. (2012), tree growth in less dry sites seems to be inherently more vulnerable to drought due to the growth-recovery allocation trade-off. This might be due to the reduction of the capacity of forests to respond to drought as the frequency and intensity of extreme droughts increases (Serra-Maluquer et al., 2018; Schwalm et al., 2017).

Site-specific versus species-specific determinism

Future species distribution in the Mediterranean Basin will depend on their ability to cope with the long-term changes in climate and their degree of tolerance to disturbances (Gea-Izquierdo et al., 2017; Reyer et al., 2013, 2015). Some broad-scale simulations on future changes in tree species distribution predict a general increase in conifer forests at the expense of broadleaf forests in the Mediterranean Basin (Keenan et al., 2011; Linder et al., 2014), although local studies contradict those projections (Galiano et al., 2010; Rigling et al., 2013). Our results did not show such clear differences among functional groups neither in the correlations with climate, nor in vulnerability to disturbances or the model projections of future species performance. In turn, the results of the GLMM underlined the higher growth capacity of larger trees, confirming that in Mediterranean rear-edge forests the rate of carbon accumulation may increase continuously with tree size (Stephenson et al., 2014). Although our modelling approach is not based on explicit ecophysiological mechanisms (e.g., Gea-Izquierdo et al., 2017) and entails evident limitations inherent to the usage of statistical models and sampling only dominant trees, it is sufficient to illustrate that the two species displaying significant declining growth trends under the *mitigation scenario* RCP2.6, beech and Scots pine, belong to different functional groups. These two species were in general the two tree species growing under more limiting climatic conditions, experiencing growth reductions and displaying the highest vulnerability to disturbances. Under the RCP2.6 scenario, the expected increase in temperature is not dramatic and most of the forests did not show significant changes in growth trends. In

turn, under the RCP8.5, most forests displayed declining growth trends concurrent with the dramatic increase in summer temperature forecasted under this scenario.

Interestingly, geographical differences were found in the tolerance to disturbances (i.e., central Mediterranean populations displayed a significantly lower recovery capacity than eastern populations) alongside with trends in tree growth (i.e., more positive growth trends in the central and eastern than western Mediterranean Basin, concurrent with less limiting climate conditions) and geographical gradients in climate sensitivity. Such spatial heterogeneity in climate is supported by the instrumental meteorological data (Fig. 7; Barkhordarian et al., 2013) and by ecological evidence (Chen et al., 2015; Dorado-Liñán et al., 2017b; Seim et al., 2014) and linked to the influence of atmospheric circulation patterns on summer climate (Dorado-Liñán et al., 2017b; Xoplaki et al., 2003). Despite this, the Mediterranean Basin is usually modelled as a rather homogeneous domain and the climate modelling exercises for the region predict a homogeneous decrease in summer precipitation and increase in aridity (e.g., Gao & Giorgi, 2008; Giorgi & Lionello, 2008).

Our results revealed the determinant influence of two atmospheric circulation patterns on the observed regional differences in forest growth and susceptibility to disturbances: (1) the PC1 synoptic pattern, centred over the Italian peninsula and linked to higher precipitation and lower temperatures in that area (**Fig. 6a,b**; Xoplaki et al., 2003); and (2) the geopotential height pattern described by the PC2 of summer precipitation (**Fig. 6c**) that represents cyclonic circulation centred in the eastern half of the Basin and linked to higher summer precipitation in the eastern Mediterranean. Such a synoptic pattern has been associated to a high summer NAO (SNAO; Folland et al., 2009), a relevant contributor to the geographical differences in summer precipitation amounts across the Mediterranean Basin during the last decades (Bladé et al., 2012).

Despite their relevant contribution to summer climate, the dynamical atmospheric circulation pattern underlying the modelled changes in temperature and precipitation under RCP2.6 and RCP8.5 did not reproduce those described by the observational data, particularly for the

precipitation patterns (**Fig. 6e-j**). Such discrepancy is severe, as future tree growth will largely depend on the precipitation amounts during summer, as shown by the homogeneous positive effect of summer precipitation on tree growth across the Mediterranean. Indeed, the unprecise representation of atmospheric circulation might be one of the reasons for the more severe growth reduction projected for eastern Mediterranean since in this area SNAO exerts a dominant influence on summer precipitation (Bladé et al., 2012). Precipitation projections suffer from large uncertainties partly due to the poor representation of dynamical mechanisms and the difficulties to correctly parametrize the internal variability of the climate system in GCMs (van Haren et al., 2013a, b). Furthermore, variations in patterns such as NAO, poorly represented in the simulated climate data as shown in **Fig 6 f, j**, are linked to other Earth subsystems such as the North Atlantic Jet (NAJ; Trouet et al., 2018); the Sahara/Sahel and West African Monsoon (WAM; Bader & Latif, 2003) and the El Niño-Southern Oscillation (ENSO; Kalimeris et al., 2017). Those systems may shift with increased anthropogenic forcing (Barnes & Polvani, 2013) and pass critical states in intensity and location, leading to large-scale impacts on human and ecological systems (so-called *tipping elements*; Lenton et al., 2008; see Schwalm et al., 2017 for a worldwide study). Thus, changes in NAJ, WAN and ENSO may promote profound changes in the state of the NAO and, hence, in the precipitation over the Mediterranean region.

Although the poor representation of dynamical mechanisms in GCMs is still a relevant issue, recent studies relying on more accurate representations of fine-scale circulation patterns have shown improved predictive skills (van Haren et al., 2015; Ozturk et al., 2015). An accurate representation of regional climatology seems to be determinant component shaping future tree growth in the Mediterranean Basin and, therefore, an essential element in forest modelling exercises. On the other hand, the classification of species in plant functional groups for modelling should take into consideration the intra-species differences in ecophysiological strategies across the distribution range, no matter if they are due to adaptations on genotype, phenotype or hydraulic strategy, and likely to move towards a classification based on site-induced adaptations instead of using biological-determinism principles.

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