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**A new multifactorial approach for studying intraannual secondary growth dynamics in
Mediterranean mixed forests: Integrating biotic and abiotic interactions.**

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Abstract

Studying intraannual growth dynamics through a modelling approach has proved useful for characterizing differences in wood phenology between species and deviations from the expected tree growth due to climate change. The aim of this paper was to determine the climatic factors and the inter- and intraspecific competition traits that drive intraannual secondary growth dynamics in three Mediterranean tree species that naturally coexist in the Spanish Northern plateau (*Pinus pinea*, *Juniperus thurifera* and *Quercus ilex*). For this purpose we obtained girth increment data from band dendrometers installed on 58 trees from May 2012 to April 2015. Half of them were located in a high-density plot and half in a low-density plot. These data were analysed through a non-linear multifactorial model considering daily and cumulative climatic effects together with inter- and intraspecific competition indices. Our results provide evidence of a spatio-temporal niche separation between species. Compared to other species, *Q. ilex* showed a wider thermal amplitude, a higher mean optimum temperature for growth and a milder effect of drought on its secondary growth. Under current climate change projections, simulations based on our model predict a secondary growth reduction for *P. pinea* and a growth enhancement for *Q. ilex* in these Mediterranean mixtures.

Keywords

Dendrometers; Mixed stands; Climate change; Non-linear mixed models; Mediterranean species;

33 **1. Introduction**

34 Mixed-species forests have gained significant attention in recent years as many studies have shown
 35 that tree species richness is a key feature for most forest functions and services (Río et al. 2016). Some
 36 studies have stressed the role of certain mixtures in the improvement of individual tree resistance and
 37 resilience (e.g. Lebourgeois et al., 2013). These benefits are not observed neither in all forest types,
 38 nor for all tree species (Grossiord et al. 2014, Merlin et al. 2015) but they are expected to be more
 39 frequent in drought-prone sites (Pretzsch et al. 2013) like Mediterranean forests. However it remains
 40 unclear how global change will modify mixed forests dynamics in the Mediterranean basin.

41 Global warming is known to alter plant phenology (Cleland et al. 2007) leading to decreases in tree
 42 radial growth in some cases (Lebourgeois et al. 2010, Natalini et al. 2015). The analysis of intraannual
 43 growth dynamics through a modelling approach has proved useful for characterizing differences in
 44 wood phenology between species and deviations from the expected tree growth due to climate change
 45 (Michelot et al. 2012). Although height growth patterns tend to be similar between coexisting tree
 46 species, this does not apply to diameter growth. Carbon assimilated by trees through photosynthesis is
 47 firstly assigned to build new photosynthetic tissues (Gea-Izquierdo et al. 2009) and primary growth,
 48 and only remaining carbohydrates are allocated to girth increment. During the growing season the
 49 timing, duration and rate of radial growth can change among species (Rossi et al. 2006) and may also
 50 change through species interactions and with varying climatic conditions.

51 The role of competition restraining individual tree growth has been widely discussed in the forestry
 52 literature, mainly by the use of competition indices. Recent studies have addressed this issue studying
 53 the role of inter- and intraspecific interactions on interannual growth (Manso et al. 2015, De-Dios-
 54 García et al. 2015). However understanding how these inter- and intraspecific interactions affect
 55 seasonal or daily tree growth in mixtures remains a challenge.

56 Studies on intraannual growth dynamics have been performed using manual band dendrometers
 57 (Martín et al. 2014), automatic band dendrometers (Urban et al. 2013), electronic point dendrometers
 58 (Zweifel et al. 2006) and core (Delpierre et al. 2016) or microcore extraction (Rossi et al. 2006). In
 59 spite of their low resolution on a daily basis, advantages from manual band dendrometers are related to
 60 their low cost of installation and maintenance (McMahon and Parker 2015) which allows to carry out

61 measurements over a larger sample of trees and during longer time spans. These methods are more
62 accurate for analysing the radial growth of the whole stem than invasive techniques like core or
63 microcore extraction and electronic point dendrometers, which can be affected by local changes in the
64 xylem or the bark (Gutiérrez et al. 2011).

65 Despite the widespread use of band dendrometers for assessing intraannual growth patterns, most
66 studies have focussed on defining patterns of seasonal dynamics and growth phenology (Urban et al.
67 2013), with only a few studies aiming to gain insight into the factors driving differences in intraannual
68 growth between trees, sites and species (McMahon and Parker 2015).

69 The effect of climatic factors on intraannual growth has usually been evaluated by means of univariate
70 analysis, such as Pearson's correlation coefficient (Grogan and Schulze 2012) or univariate regression
71 models, which focus on an assumed linear relation among the studied effect and a single factor at each
72 time. However, understanding the effect of multiple factors as well as their complex interactions on
73 growth should be approached through more complex multivariate and non-linear models (Paine et al.
74 2012).

75 Our aim was to determine the climatic factors and the inter- and intraspecific competition traits that
76 drive intraannual secondary growth dynamics in three Mediterranean tree species, *Pinus pinea* L.,
77 *Quercus ilex* subsp. *ballota* (Desf.) Samp., and *Juniperus thurifera* L., co-occurring in mixed forests in
78 the Spanish Northern Plateau, by means of a modelling approach. The specific objectives of this
79 analysis were (a) to determine the competition factors that define the daily potential secondary growth
80 of the subject tree; (b) to elucidate the main climatic factors that limit the daily potential girth
81 increment for each tree species coexisting in *P. pinea* mixed stands. Our first hypothesis was that the
82 effect of inter- and intraspecific competition on potential growth would be different for each species,
83 *P. pinea* being more competitive than *J. thurifera* and *Q. ilex* subsp. *ballota* both with conspecific
84 trees and with the other tree species (De-Dios-García et al. 2015). In line with other studies (Mayoral
85 et al. 2015) our second hypothesis was that *Q. ilex* subsp. *ballota* (hereafter *Q. ilex*) would reach its
86 optimum growth conditions at higher temperatures than *P. pinea* and *J. thurifera*. Our third hypothesis
87 was that *Q. ilex* would be more tolerant to summer drought than the other tree species (Mayoral et al.

2015), achieving higher girth increments in relative terms than *P. pinea* and *J. thurifera* during the dry season.

2. Material and methods

2.1. Data collection

2.1.1. Study area

The study area is located in the Carrascal state forest (41°36'N, 4°19'W), in a flat zone within the limestone plain areas in the east of the province of Valladolid, in the Spanish Northern Plateau. The elevation is around 885 m, the average annual precipitation is highly variable ranging from 220 to 630 mm and it mainly falls during autumn and spring. The mean annual temperature is 11 °C, reaching maximum average values of 37 °C in the warmest months (July and August) and minimum average values of -5 °C in the coldest ones (December and January), according to historical data (1975-2010) from Valladolid meteorological station (www.aemet.com). The area has a Mediterranean continental climate with a characteristic hot and dry summer period during which mean monthly precipitation is 21 mm. The main types of soils are inceptisols with an average water holding capacity of 176 mm/m. In the province of Valladolid, *P. pinea* occupies 74 000 ha (29 000 ha are pure stands, 33 000 are mixed stands with other conifers and 12,000 ha are mixed stands with hardwoods). Mixed stands with hardwoods represent the most diverse and complex forest systems in the region and are mainly located in limestone plain areas. The present study focused on these more complex admixtures, where *Pinus pinea* grows with *Quercus ilex* and *Juniperus thurifera*.

Land ownership has played a critical role in the maintenance of mixed broadleaf-conifer forests in the Spanish Northern Plateau, where *P. pinea*, *P. pinaster*, *Q. ilex*, *Q. faginea* and *J. thurifera* naturally coexist. Nowadays most of these structurally complex admixtures are found on land that was privately owned until the 1980s. The lack of investments from private owners and the absence of management plans contributed to the preservation of these mixtures. Most of this land was sold to the regional government in the 1980s. At that time, management in mixtures began to focus on a tree selection system, promoting growth and regeneration of all tree species. Conservation of biodiversity is the main management objective in these forests, together with other ecosystem services such as cone and nut production, timber and biomass, mushrooms and recreational uses.

2.1.2. Experimental design – dendrometer measurements

Data were collected from two adjacent 50 m x 60 m plots placed in two contrasting stocking densities: A high density plot (basal area $G=18.8 \text{ m}^2/\text{ha}$), which is located in a wildlife corridor that has not been managed since the 1970s and a low density plot (basal area $G=9.6 \text{ m}^2/\text{ha}$), where the last forest management intervention was carried out in 2002. Within each plot, the coordinates of all trees with height greater than 1.30 m were recorded during the summer of 2011. During that measurement as well as in the subsequent measurements, diameter at breast height (dbh), stump diameter, total height, height to crown base, and four perpendicular crown radii measured in cardinal directions were recorded for each tree. Stand attributes are shown in Table 1.

Intraannual girth increment was measured by means of band dendrometers (Dendrometer Increment Sensor DB20 EMS Brno, (www.emsbrno.cz), which were mounted at breast height (1.30 m) on 58 trees (dbh > 5cm) after leveling off the bark with a rasp. In order to have a balanced design the dendrometers were split half and half between the high density plot (HDP) and the low density plot (LDP). We selected a balanced representation of the whole range of tree diameters observed in the study area for each tree species. We monitored the secondary growth of 21 *P. pinea* trees (12 in the HDP and 9 in the LDP), 13 *Q. ilex* trees (5 in the HDP and 8 in the LDP) and 24 *J. thurifera* trees (12 in the HDP and 12 in the LDP). The dendrometer bands were revisited on 59 occasions on a regular basis (average period 17 ± 6 days) from May 2012 to April 2015 and the girth of each tree was measured with a precision of 0.1 mm. To avoid diurnal biases due to changes in tree water status (Baker et al. 2002), all measurements were taken at around 11 am. Details on the characteristics of the selected trees are listed in Table 2.

Daily climatic variables including mean, maximum and minimum temperatures, daily precipitation, days without precipitation and days with frost were gathered from a meteorological station located in the area of study (41°34'N, 4°20'W, 2.5 km from the study site) and managed by the local forest service. 5.9% of absent data were estimated using data from Valbuena de Duero meteorological station (41°38'N, 4°17'W, 6 km from the study site), which are available from www.inforiego.org.

2.2. Data analysis and statistical methods

2.2.1. *Modelling approach*

Due to the hierarchical structure of the data, three indices were defined, i, j and s , which represent the tree, the time interval between measurements and the species, respectively. We chose the girth increment (mm) as the response variable (gi_{ijs}). It was defined as the difference between the girth observations in two consecutive measurements. Since our objective was to study the effects involved in wood expansion at breast height, we smoothed our original dendrometer series (Delpierre et al. 2016) by specifying that no shrinkage in girth increment was allowed, thus negative values for gi_{ijs} were set to zero. A logarithmic transformation was applied to comply with the assumption of normality and homogeneous variances:

$$y_{ijs} = \text{Log}[(gi_{ijs} \cdot 10) + 1] \tag{1}$$

We assumed there were some daily potential effects acting at tree level that define a theoretical daily maximum secondary growth and climate covariates that limit this potential growth. The daily potential effects (PE_{is}) represent the expected growth when the other factors are at optimal values. Thus, the sum of the daily effects over the time interval j can be used to predict the total secondary growth during this interval.

Among the PE_{is} , we included tree-level covariates: inter- and intraspecific competition indices ($AOI_{inter,is}$, $AOI_{intra,is}$), dbh_i and a species effect (see eq. 2). We used the area overlap distance dependent competition indices (AOI) developed by Bella (1971) and later modified by Tomé and Burhart (1989) to define inter- and intraspecific interactions between the trees of the area of study. Further details on the description and use of these indices are annexed to this paper (See Appendix).

Given the hierarchical structure of the data, it could be suspected that there would be a violation of the assumption of independence. In order to account for this assumption, a tree random effect (u_i) was included on the intercept. We assumed that the differences in stand density among both two plots were accounted for by the inter- and intraspecific competition indices. Additionally, since both plots were

adjacent, we did not consider the inclusion of a random plot effect accounting for unobservable effects due to differences in site conditions.

$$PE_{is} = \alpha_s + (\beta_s \cdot AOI_{inter,is}) + (\gamma_s \cdot AOI_{intra,is}) + (\theta_s \cdot dbh_i) + u_i \quad (2)$$

where the terms α , β , γ , θ are estimable, in some cases species-specific, parameters, $AOI_{inter,is}$ and $AOI_{intra,is}$ stand for inter- and intraspecific competition, respectively, for tree i of species s , dbh_i is the diameter at breast height of tree i and u_i is a tree random effect, so that $\mathbf{u} \sim N(0, \sigma_u^2)$, σ_u^2 being the variance of the tree random effects.

As regards the climate predictors we considered thermal covariates such as the days since the last frost event, daily mean and maximum temperatures ($T_{av,m}$, $T_{max,m}$ in °C) and water availability-related variables based on daily precipitation and on days since the last precipitation event. Climate variables were grouped into a temperature effect, a frost effect and a drought effect (see eq. 3). Thereby the cumulative effects CE_{ijs} affecting girth increment of tree i of species s over interval j were defined as:

$$CE_{ijs} = PE_{is} \sum_m TE_{ms} \cdot FE_{ms} \cdot DE_{ms} \quad (3)$$

where m extends from the first day to the last day of the increment period j , PE_{is} represents the potential effects as defined in eq. 2 and TE_{ms} , FE_{ms} and DE_{ms} represent the temperature, frost and drought effects at the day m on species s , respectively. These three effects were expressed as non-linear functions of climatic variables.

The functions were designed to range from 0 (total inhibition of potential growth) to 1 (growth reaches all its potential). Stem growth response to temperature can adopt different shapes depending on the species and can even vary between subspecies of the same genus (Lempereur et al. 2015, Mayoral et al. 2015). We chose a Gaussian function for the temperature effect since it had been found adequate in other modelling approaches for *Q. ilex* subsp. *ballota* and *P. pinea* in mixed and monospecific *P. pinea* forests in the Iberian peninsula (Manoso et al. 2013, Mayoral et al. 2015) under similar climatic conditions as in our study site. The function can be expressed as follows:

$$TE_{ms} = \exp \left[- \frac{(T_m - \mu_s)^2}{\sigma_s^2} \right] \quad (4)$$

where T_m is either daily average temperature ($T_{av,m}$) or daily maximum temperature ($T_{max,m}$), μ_s stands for optimum daily average temperature ($\mu_{av,s}$) or optimum daily maximum temperature ($\mu_{max,s}$) for species s , σ_s^2 represents the variance of the normally distributed response of secondary growth to T_m for species s .

In the case of frost and drought, we assumed they would have a long lasting effect on secondary growth. Freezing was thought to inhibit girth increment as a function of the number of days since the last frost, with the maximum growth reduction on the very day the frost event occurred. Hence, it was parametrised as:

$$FE_{ms} = 1 - \exp(\varphi_s \cdot DF) \quad (5)$$

where φ_s is the parameter associated to the frost effect on species s , which was expected to adopt negative values; DF stands for days since the last frost.

In regard of drought effects, two approaches were tested (eq. 6.1 and eq. 6.2.1):

$$DE_{ms} 1 = \exp(\lambda_s \cdot DP) \quad (6.1)$$

$$DE_{ms} 2 = 1 - \exp(\delta_s \cdot WR_m) \quad (6.2.1)$$

$$WR_m = (P_m + WR_{m-1}) \exp(\lambda \cdot DP) \quad (6.2.2)$$

where DE_{ms} is the drought effect on species s on day m , DP are the days since the last precipitation event. For the second approach, WR_m is a proxy for the daily water reserve on day m , and is iteratively computed considering precipitation on day m , P_m , the value of WR_m in the previous day $m-1$, and DP. λ_s and δ_s are two specific parameters approaching how soil water content diminishes as days without precipitation increase, thus they should adopt negative values.

The combination of the climatic effects and the daily potential, as shown in eq. 3, yields the cumulative effects CE_{ijs} that we tried to use as a predictor of gi_{ijs} . After preliminary checks of the residuals, we found out that a log-transformation of CE_{ijs} was needed, the resulting model being as follows:

$$\text{Log}[(gi_{ijs} \cdot 10) + 1] = \text{Log}(CE_{ijs} + 1) + \epsilon_{ijs} \quad (7)$$

where ϵ_{ijs} is the error term such that $\epsilon_{ijs} \sim N(0, \sigma^2)$, with σ^2 the residual variance.

2.2.2. *Model fitting*

The model was fitted using a maximum likelihood estimator. We followed a sequential procedure to select the effects entering the model: (i) competition and size factors determining daily potential growth, (ii) thermal effects, (iii) drought related effects, (iv) random effects, (v) species specific climatic responses. Preliminary models attained at each step of the model construction were compared in terms of bias (standardized residuals plotted against time), level of significance of the parameter estimates included and three different criteria for model comparison (Akaike information criterion, Bayesian information criterion and minus twice the maximum log-likelihood). At each step, the residuals were checked to identify heteroscedastic patterns. All calculations were carried out using PROC NLMIXED in SAS 9.2. (SAS Institute Inc. 2009).

2.2.3. *Model evaluation*

The model evaluation was primarily carried out by computing goodness-of-fit statistics such as mean error (E), root mean square error (RMSE) and modelling efficiency (MEF), computed over the residuals in real scale. The model was evaluated at different scales: whole data-set, per species, per plot and per combination of species and plot. A second evaluation was based on visual comparison of the girth increment trajectories between observed and predicted values. Finally, the accuracy of the model in predicting cumulative girth increment at tree level for the whole period was also tested at different scales by means of E, RMSE and MEF. We performed a t-test on the mean error under the null hypothesis that the model was correct, i.e. E was equal to 0. Consequently, any significant probability could be interpreted as a lack of fit. Evaluation of the model was carried out over raw, non-transformed values, thus antilogarithmic back-transformation of predicted values was carried out by multiplying the exponential of the predicted value per 0.5 times the variance of the error terms (Duan 1983).

2.2.4. *Model validation*

We did a model validation over a set of trees from the two plots included in the assay. The growth increment data used for the validation was obtained from cores and cross section slices extracted in 2011, thereby corresponding to different years than the ones considered to study girth increment (2012-2015). These cores and cross section slices were obtained from a representative sample of trees

covering the whole range of diameters identified in the area of study. Total number of trees used in the validation were 48 *P. pinea* (24 per plot), 15 *J. thurifera* (7 from the low density plot, 8 from the high density plot) and 4 *Q. ilex* (2 per plot). *Q. ilex* trees used for the validation had to be felled, which explains the lower amount of *Q. ilex* trees used for the validation compared to the other species. Model validation was based on computing the Pearson's correlation coefficient between the observed values of the annual radial increment (taken from increment cores and cross section slices) and the predicted annual girth increment obtained from our model. Temporal extent of the validation covered from 1997 to 2011 (15 years). Correlation coefficients were thus computed using the 15 observed-predicted annual values for each tree. We did not convert annual girth increment data into annual radial increment since girth measurements take into account bark growth but core increments do not.

2.2.5. *Growth projections under current and forecasted climate scenarios*

The final model was used to predict annual girth increment for the three species comparing current climate data with simulated climate data from IPCC RCP 8.5 climate scenario for 2075. Daily climate data were obtained from AEMET projections using climate model ACCESS 1-0 (http://www.aemet.es/es/serviciosclimaticos/cambio_climat/datos_diarios), resulting in a 4.5-°C increase of the average temperature, and a 30% decrease in annual rainfall. For this simulation competition was not considered.

3. Results

3.1. Definition of secondary growth function

The sequential process of construction of the models for the secondary growth is shown in Table 3. At each step of the model construction a new factor was included and compared in terms of -2LL, AIC and BIC with the same model without this effect. Among the main constant factors determining the daily potential growth tree dbh was discarded as it was only significant for *J. thurifera* and it did not improve the performance of the model either (models [1] and [2]). Hence, daily potential girth increment was defined by a species effect in the intercept and inter- and intraspecific competition indices. With respect to thermal effects, mean daily temperature resulted in a best fit than maximum temperature (models [3] and [4]). Integrating the frost effect did not improve the model significantly,

consequently the frost effect was removed in the process of model construction (models [4] and [5]). However both drought approaches tested were significant. Drought effect 2 was chosen in preference to drought effect 1 since it improved the model fit in terms of AIC, BIC and -2LL when compared with the same model with drought effect 1 (models [6]-[7]). The inclusion of a tree random effect resulted in a significant improvement in terms of AIC, BIC and -2LL (models [7] and [8]). We finally tested the different alternatives of inclusion of specific interactions on the climatic effects (models [9]-[15]). The fit of the complete model [15] could not be attained due to convergence problems. Comparison among models [9]-[14] resulted in very minor differences. We finally opted to select the model [12], including specific parameters for thermal amplitude and drought effect and a common parameter for drought occurrence, as it can be considered a good compromise between goodness of fit and parsimony in the number of parameters entering the model. Table 4 presents the parameter estimates of the preferred model.

3.2. Factors affecting intraannual growth patterns

The final girth increment model produced a hyperplane, depending on biotic and abiotic interactions from which we could infer contrasting growth responses by species for the different factors. Growth patterns were characterized by a succession of sharp increases followed by plateaus, which corresponded to growth increments during spring and fall periods and growth cessation in summer and winter times, respectively (Fig. 1).

3.2.1. Daily potential effects

The species effect on the intercept (α_s) was significant for the three species implying different average girth increments for each of them. The effect was greater for *P. pinea* ($\hat{\alpha}_1 = 3.5498$), followed by *Q. ilex* ($\hat{\alpha}_2 = 2.0815$) and *J. thurifera* ($\hat{\alpha}_3 = 1.9852$). Concerning interspecific competition, significant values were observed for *Q. ilex* (P-value = 0.034) and close to significant for *J. thurifera* (P-value = 0.055), being growth inhibition larger for *Q. ilex* ($\hat{\beta}_2 = -0.09597$) than for *J. thurifera* ($\hat{\beta}_3 = -0.05453$). Interspecific competition effect was not significant for *P. pinea* (P-value = 0.527). With respect to intraspecific competition we obtained a significant inhibition of the potential girth increment for *P. pinea* (P-value = <0.001) and *J. thurifera* (P-value = 0.010), being more than two times lower for *P.*

pineta ($\hat{\gamma}_1 = -0.1692$) than for *J. thurifera* ($\hat{\gamma}_3 = -0.3425$). The effect of intraspecific competition was non-significant for *Q. ilex* (P-value = 0.409).

3.2.2. Climate covariates

As regards the temperature effect, optimum daily average temperatures for secondary growth were 16.4 °C for *P. pineta* ($\hat{\mu}_1$), 32.0 °C for *Q. ilex* ($\hat{\mu}_2$) and 17.8 °C for *J. thurifera* ($\hat{\mu}_3$). The scaled normally distributed response of girth increment to daily average temperature differed between species, being three times greater for *Q. ilex* ($\hat{\sigma}_2^2 = 210.3400$) than for *J. thurifera* ($\hat{\sigma}_3^2 = 67.4487$) and *P. pineta* ($\hat{\sigma}_1^2 = 64.7046$) pointing to a wider thermal amplitude for *Q. ilex* than for the other tree species. The symmetric thermal intervals, together with the optimum average temperatures and different thermal amplitudes by species, can be seen in Fig. 2a. With respect to the drought effect on girth increment, it differed across the species, being more limiting for the intraannual secondary growth of *P. pineta* ($\hat{\delta}_1 = -0.1382$) and *J. thurifera* ($\hat{\delta}_3 = -0.1123$) than for *Q. ilex* ($\hat{\delta}_2 = -0.2559$). To facilitate the interpretation of the drought effect, we ran a simulation considering initial water reserve values of 0 and a single episode of precipitation of 5 mm on the first day of the simulation (Fig. 2b). Lower values obtained for the drought effect for *P. pineta* (0.4989) and *J. thurifera* (0.4297) than for *Q. ilex* (0.7218), the first day of the simulation imply that *Q. ilex* makes better use of water than the other two species after an isolated rainfall event when soil water reserves are scarce.

3.3. Model evaluation

Accuracy of the model was first evaluated by means of common statistics as mean error, root mean square error and modelling efficiency, for the whole data set, and separately for each plot, species and each combination of plot and species (Table 5). Non-significant P-values under the null hypothesis that the mean error (E) = 0 imply that the difference between observed and predicted values is non-significant and thereby there is no systematic bias in the predictions. Model predictions of girth increment were unbiased for all levels of grouping. At global scale, RMSE reached 0.694 mm, with MEF over 33.4%. We obtained more accurate predictions for the HDP than for the LDP, especially for *Q. ilex*, and *J. thurifera*. The main part of the observed bias was associated with *P. pineta* girth

increment in the LDP. This result is mainly due to the unexpected larger summer growth in 2014 observed in three pines in the LDP.

The visual agreement between average observed and predicted increment trajectories through the whole cycle (Fig. 1), perfectly mimicking the bimodal growth patterns, again points to a better performance of the model in the HDP than in the LDP, particularly for predicting the secondary growth of *Q. ilex* and *J. thurifera*.

We finally tested the ability of the model to predict the cumulative girth increment of the 58 trees evaluated along the whole period of study (1 062 days). Unbiased predictions were obtained for all scales evaluated (Table 6, Fig. 3). The combinations of plot and species could not be tested due to the small number of trees involved in some combinations. The accuracy of the model was greater in predicting the girth increment in the HDP, than in the LDP, especially for *J. thurifera*. Once more, higher RMSE values for *P. pinea* are due to the unexpected summer growth of three dominant trees (Fig. 3). However, MEF reached values over 86% and RMSE below 5.6 mm for all the scales studied, showing a high agreement between observed and predicted values, and a notable long-term model accuracy.

3.4. Model validation

Model validation showed a clear agreement between observed annual increment data obtained from cores and cross section slices and the values of annual girth increment predicted using the model (Table 7). The main part of the tree-level correlations (63 out of 67) between observed radial increment and predicted girth increment were positive and statistically significant. Average correlation values ranged from 0.40 – 0.55 for all the species and plots, with maximum values of 0.57 – 0.75 depending on the species. Models for *P. pinea* and *Q. ilex* performed better in the high-density plot, while models for *J. thurifera* performed better in the low-density plot.

The model mimicked the pattern of interannual variability in radial increment (Fig. 4), especially in the last years of the simulation (2005-2011). However, the model was not able to match perfectly the effect of the 2002 thinning carried out in the low density plot, since we predicted a 2-year delayed response with respect to the real observed values (Fig. 4a, 4b and 4c).

3.5. Growth projections under changing climate scenarios

The results from our simulations under current climate and RCP 8.5. climate scenario indicate secondary growth reductions of 19.1 % for *P. pinea* and 6.5 % for *J. thurifera* and a growth increase of 61.6 % for *Quercus ilex* under these simulated climate projections (Fig. 5). We would like to stress that competition was not considered for this simulation as the definitive model [12] only had slightly lower values in terms of minus twice the maximum log-likelihood (-2LL=8650) when compared with the same model without competition (-2LL=8689). Including competition at tree level also implied solving many technical problems when running the simulations. Thereby these growth projections are referred to open grown trees and must be treated with caution.

4. Discussion

4.1. Advantages from a multifactorial non-linear approach for intraannual tree growth studies

Linear correlations between growth estimates and different climatic variables (Camarero et al. 2010, Michelot et al. 2012) and linear mixed models (e.g. Martín et al., 2015) have been used to study intraannual growth dynamics. However many climate-growth interactions are known to be non-linear. Previous studies have also highlighted the need of integrating both competition and climatic data for intraannual tree growth studies (Gutiérrez et al. 2011). In the Mediterranean areas many climatic factors like high temperatures, elevated transpiration and soil water depletion intervene simultaneously constraining intraannual girth increment. We thereby propose a non-linear multifactorial approach that can cope with all this limitations allowing us to understand the ecological needs of different species at one time.

4.2. Intraannual growth patterns

Many studies have found different growth dynamics in pine and oak species during the growing season concerning the date of budburst, leaf unfolding, radial growth onset and cessation, secondary growth rates or contrasting patterns of carbon allocation (e.g. Michelot et al., 2012; Zweifel et al., 2006). Girth increment data obtained from band dendrometers have limitations to identify some phenological events due to the reversible stem shrinking and swelling. However, we believe our model

represents a good alternative to study girth increment based on daily and cumulative climatic effects as it only considers stem growth with stem shrinkage set to values of zero. Model predictions for cumulative girth increment were unbiased and show a notable long-term model accuracy. The general growth rates of the three tree species we studied (Ruiz de la Torre 2006) indicate that *P. pinea* has the highest potential girth increments followed by *J. thurifera* and *Q. ilex* which is consistent with the intercept values we obtained. Previous studies in the Iberian peninsula (Campelo et al. 2007b, Camarero et al. 2010, Martín et al. 2014) have reported bimodal growth patterns for the three species over the year, characterized by a succession of sharp growth increases followed by plateaus, which is in line with our results. Diameter growth increased mainly during spring and autumn, coinciding periods of higher precipitation, increased soil water reserves and milder temperatures for growth (Pinto et al. 2011). Girth increment was repressed in summer, which is in agreement with a growth inhibition by high average temperatures and soil water deficit during the summer (Campelo et al. 2009). Secondary growth also stopped in winter, probably due to cambial dormancy caused by low average temperatures (Liphschitz et al. 1984, Gea-Izquierdo et al. 2009) and photoperiod shortening (Cherubini et al. 2003).

4.3. Size effects and intraannual competition differences between and within species

We obtained significant growth restrains by interspecific competition for *J. thurifera* and *Q. ilex*. Interspecific competition was also size-symmetric (De-Dios-García et al. 2015), implying that resource uptake is independent of target tree sizes and takes place mainly for belowground resources (Schwinning and Weiner 1998). However interspecific competition was not significant for *P. pinea* on a daily basis. Juniper trees seem to develop shallower root systems in drought stressed sites than co-occurring pine species (Willson et al. 2008) while Mediterranean oaks tend to develop large taproots reaching deeper soil layers when growing in drought-prone environments (Canadell et al. 1996). We further obtained competitive reduction for *J. thurifera*, interspecific interactions being less intense than intraspecific interactions, which is another proof of niche partitioning and interspecific differentiation in resource use (Forrester 2014).

Intraspecific competition was significant for *J. thurifera* and *P. pinea* having in both cases a negative impact on secondary growth. Intraspecific interactions, as defined by the competition index (De-Dios-

García et al. 2015), were also size-asymmetric, indicating that larger trees benefit from a larger part of the resources, which limits the growth of their smaller conspecific neighbours (Schwinning and Weiner 1998). However and contrary to our third hypothesis, the effect of intraspecific competition on girth increment was two fold in *J. thurifera* compared to *P. pinea*. Low levels of intraspecific competition imply complete growth cessation for *J. thurifera*, but not for *P. pinea*. The more limiting effect of intraspecific competition on *J. thurifera* secondary growth could be due to their clumped spatial pattern (unpublished data) found in the field around bigger *P. pinea* trees. In the case of the evergreen oak *Q. ilex* intraspecific competition indices were not significant. A large scale study on the 15 most important tree species in the Iberian peninsula indicated that Mediterranean evergreen broadleaved species were the least sensitive to competition in terms of growth (Gómez-Aparicio et al. 2011). Another explanation for this result might be the low diameters found for *Q. ilex* in these forests that were intensively coppiced for fuelwood and charcoal production until 1950s, constituting nowadays mainly a coppice forest.

4.4. Secondary growth responses to climate are species dependent

Previous studies state that the main climatic effects constraining intrannual secondary growth of *Q. ilex* are temperature at short time scales (Gutiérrez et al. 2011) and water availability (Corcuera et al. 2004, Martín et al. 2014), which were both significant in our study. *J. thurifera* is also known to have a pronounced phenological activity, with a strong cambium dormancy in xeric sites during summer and a radial growth resumption due to cambium reactivation following late-summer and autumn rainfalls (Camarero et al. 2010). We obtained higher autumn girth increments for *J. thurifera* than for *Q. ilex*. Autumn precipitation events are known to moisten only the most superficial soil layers in Mediterranean continental areas (Camarero et al. 2010). Since *J. thurifera* roots are mainly developed in the upper soil profile, this may provide them a competitive advantage, allowing them to invest more resources on diameter growth than co-occurring pines and oaks during the autumn season. As regards *P. pinea*, latewood formation, which occurs during the summer, is limited by drought stress and extreme temperatures (Campelo et al. 2007b).

Recent studies on mixed *P. pinea* stands in the Spanish central range have identified higher optimum temperatures for photosynthesis for *Q. ilex* than for *P. pinea* and other *Juniper* species (Mayoral et al.

2015), which are consistent with the optimum temperatures for growth that we obtained for each of these species. These results are also in accordance with a more thermophilic and light demanding strategy for *Q. ilex* than for *P. pinea* and *J. thurifera* trees. However, studies on intraannual growth in other *Pinus* and *Quercus* species indicate that the carbon fixed through photosynthesis is not directly used for radial growth in above-ground wood, evidencing that the early phase of radial growth completely depends on internal C-stores (Zweifel et al. 2006).

The wider thermal amplitude obtained for *Q. ilex*, compared with *J. thurifera* and *P. pinea* confirms the eurythermic character of this species, as it had been previously outlined in the literature (Ruiz de la Torre 2006), capable of maintaining secondary growth along a wide thermal range. Gea-Izquierdo et al. (2009) found a negative correlation between high temperatures and growth for *Q. ilex*. Our results indicate that considering only elevated temperatures is not sufficient to explain this growth suppression. A combined effect of high temperatures, elevated evapotranspiration and soil water stress could cause the secondary growth inhibition, as observed in this study.

Drought effect was significant and inhibited growth for all species. However it was less limiting for *Q. ilex* than for *J. thurifera* and *P. pinea*. Other studies have found different growth responses to drought events between pine and oak species, oaks being more resistant to summer droughts and pine species being more resistant to spring droughts (e.g. Morán-López et al., 2014). Pine trees are known to unfold their needles during the summer and can attain one fourth of the total annual radial growth by the time their leaves reach full expansion (Zweifel et al. 2006). However summer droughts, which were the main drought events that occurred during the period of study, can strongly affect the secondary growth of pines since they hamper needle formation and cell enlargement reducing their radial increment (Merlin et al. 2015). Furthermore, both *Q. ilex* and *J. thurifera* are known to profit from isolated summer rainfalls (Corcuera et al. 2004, Camarero et al. 2010, Gutiérrez et al. 2011) activating xylogenesis and expanding their radial growth forming double rings (Campelo et al. 2007a). As opposed to this, *P. pinea* cannot benefit from this water supply during the driest months of the year (Campelo et al. 2007b). This behaviour in *Q. ilex* is particularly interesting in trees living in a Mediterranean continental area. Diameter growth during the summer has been observed in *Q. ilex* trees living in more mesic locations (Cherubini et al. 2003). However, studies from open *Q. ilex* woodlands

in continental sites in the Iberian peninsula, with similar precipitation regimes and lower stand densities obtain opposite growth tendencies with respect to late-summer precipitations (Gea-Izquierdo et al. 2009). We hypothesize that similar precipitation regimes in Mediterranean continental sites may be more favourable in mixed forests, due to niche complementarity, leading to less water-stressed conditions in the summer for evergreen broadleaf trees.

4.5. Model validation and growth projections

There is a marked recent tendency towards drier and hotter summer seasons in the region of study according to historical data (1975-2010) from Valladolid meteorological station (www.aemet.com). The model was constructed with data from 2012-2015, therefore considering more similar climate conditions to the ones found in the last period of the validation (2005-2011). The low density plot was also subjected to thinning practices to reduce stand density in 2002. The effect of thinning on the secondary growth of remaining trees was not considered in the model, which was constructed with girth increment data from 2012-2015, ten years after the thinning treatment was applied. We believe this may explain the poorer model performance in the first years of the validation and the more accurate growth predictions three years after the thinning treatments were applied.

According to our model projections for 2075 the 4.5 °C increase on average temperature and 30% decrease in annual rainfall expected in the region of study will negatively affect the secondary growth of *P. pinea*. If competition were included in these projections, intraspecific competition may even be translated in lower secondary growths for *P. pinea*. *Q. ilex* will be favoured maybe due to its wider thermal amplitude; however reduced growth could be expected if interspecific competition were considered. *J. thurifera* will remain practically unaffected but may have slight growth reductions including inter- and intraspecific competition.

4.6. Conclusions

Forest managers should be cautious to extrapolate these results at a forest management scale due to the low explained growth variance, particularly for *P. pinea* growing in mixed stands in low densities. However our predictions for cumulative girth increment show a notable long-term model accuracy. We thereby believe that this model is a useful tool to describe the effect of inter- and intraspecific competition and different climate change scenarios on secondary growth and may help orientate forest

management decisions. Current management practices in the Spanish Northern Plateau have favoured *P. pinea* over *Q. ilex*. Based on all the previous findings and in accordance with the simulations carried out with the model for future climate scenarios, forest managers may wish to modify their management schedules lowering *P. pinea* stand densities and promoting species like *Q. ilex* in mixtures, with a higher plasticity in response to climatic conditions during the growing season (Gutiérrez et al. 2011). In line with other authors (Gea-Izquierdo et al. 2009), we believe this would be a more balanced stand combination in sclerophyllous oak-conifer mixtures, better adapted to the expected change in climatic conditions.

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Table 1. Stand attributes, estimated using trees with diameter at breast height ≥ 5 cm. N: stand density; G: basal area; Dg: quadratic mean diameter; H: mean total height; LDP: low density plot; HDP: high density plot.

		LDP	HDP
N (stem/ha)	Total	383	943
	<i>P. pinea</i>	83	497
	<i>Q. ilex</i>	163	147
	<i>J. thurifera</i>	137	253
G (m ² /ha)	Total	9.6	18.8
	<i>P. pinea</i>	7.2	16.8
	<i>Q. ilex</i>	0.9	0.5
	<i>J. thurifera</i>	1.4	1.5
Dg (cm)	<i>P. pinea</i>	33.3	20.7
	<i>Q. ilex</i>	5.0	6.7
	<i>J. thurifera</i>	10.2	8.8
H (m)	<i>P. pinea</i>	9.1	7.2
	<i>Q. ilex</i>	4.5	4.2
	<i>J. thurifera</i>	5.4	5.3

Table 2. Characteristics of the 58 trees with band dendrometers. Diameter classes correspond to: II=5cm≤D<10cm, III=10cm≤D<15cm, IV= 15cm≤D<25cm, V= 25cm≤D<35.

Species	Site	Diameter class	Number of trees	Range of tree heights (m)	Range of dbh (cm)
<i>Pinus pinea</i>	High density	III	4	6.2-7.1	12.65-14.95
		IV	4	7.5-9.3	23.2-24.8
		V	4	9.6-10.4	25.5-34.35
	Low density	III	1	4.7-4.7	12.25-12.25
		IV	4	5.6-8.2	18.05-24.25
		V	4	8.5-10.8	28.45-34.3
<i>Quercus ilex</i>	High density	II	4	3.7-5.4	7.5-9.15
		III	1	6-6	10.85-10.85
	Low density	II	5	3.4-4.7	5.6-9
		III	3	4.9-5.3	10.05-10.9
<i>Juniperus thurifera</i>	High density	II	4	5.3-7.8	8.8-9.65
		III	6	5.6-8.7	11.1-14.85
		IV	2	8.5-9	17.7-20.6
	Low density	II	4	3.7-6.1	6.75-9.6
		III	4	5.6-7.1	11.35-14.35
		IV	4	7.2-8.8	16.9-24.8

Table 3. Comparison of fitting statistics and sequential procedure for model construction. Intrasp.: Intraspecific; Intersp.: Interspecific; dbh_i: diameter at breast height of the target tree i ; $T_{\max}$: daily maximum temperature; T_{av} : daily average temperature; α_s is the intercept for species s ; β_s : parameter associated to interspecific competition for species s ; γ_s : parameter associated to intraspecific competition for species s ; θ_s : parameter associated to diameter at breast height of the target tree of species s ; μ_s : optimum daily temperature for species s ; λ : parameter related to drought occurrence; λ_s : parameter related to drought occurrence for species s ; δ : parameter linked to the drought effect; δ_s : parameter linked to the drought effect on species s ; σ^2 : variance of the scaled normally distributed response of secondary growth to daily temperature; σ_s^2 : variance of the scaled normally distributed response of secondary growth to daily temperature for species s ; σ_{ui}^2 : variance linked to the tree random effect; -2LL: -2 log likelihood; AIC: Akaike information criterion; BIC: Bayesian information criterion.

Modelling step	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Intercept	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s
Intersp. competition	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s
Intrasp. competition	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s
dbh _i	θ_s	-	-	-	-	-	-	-	-	-	-	-	-	-	-
$T_{\max}$	-	-	μ_s	-	-	-	-	-	-	-	-	-	-	-	-
T_{av}	-	-	-	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s
Frost effect	-	-	-	-	φ	-	-	-	-	-	-	-	-	-	-
Drought occurrence	-	-	-	-	-	λ	λ	λ	λ	λ	λ_s	λ	λ_s	λ_s	λ_s
Drought effect	-	-	-	-	-	-	δ	δ	δ	δ_s	δ	δ_s	δ	δ_s	δ_s
Thermal amplitude	-	-	σ^2	σ^2	σ^2	σ^2	σ^2	σ^2	σ_s^2	σ^2	σ^2	σ_s^2	σ_s^2	σ^2	σ_s^2
Random tree effect	-	-	-	-	-	-	-	σ_{ui}^2	σ_{ui}^2	σ_{ui}^2	σ_{ui}^2	σ_{ui}^2	σ_{ui}^2	σ_{ui}^2	σ_{ui}^2
-2LL	10 124	10 134	9 570	9 500	9 489	8 942	8 718	8 668	8 656	8 663	8 661	8 650	8 647	8 660	-
AIC	10 150	10 154	9 598	9 528	9 519	8 972	8 750	8 702	8 694	8 701	8 699	8 692	8 689	8 702	-
BIC	10 230	10 215	9 684	9 614	9 611	9 063	8 848	8 737	8 733	8 741	8 738	8 735	8 733	8 745	-

Table 4. Summary of parameter estimates for the definitive model [12], where subscripts: 1 = *P. pinea*, 2 = *Q. ilex*, 3 = *J. thurifera*. α is the intercept for species 1, 2, 3; β is the parameter associated to interspecific competition for species 1, 2, 3; γ is the parameter associated to intraspecific competition for species 1, 2, 3; δ is the parameter linked to the drought effect on species 1, 2, 3; λ is the parameter related to drought occurrence; μ represents the optimum daily average temperature for species 1, 2, 3; σ^2 stands for the variance of the scaled normally distributed response of secondary growth to daily average temperature for species 1, 2, 3; σ^2_{ui} is the variance linked to the tree random effect.

Parameter	Estimate	Stand. error	Df	t-Value	p-Value
α_1	3.5498	0.5647	57	6.29	<0.001
α_2	2.0815	0.6622	57	3.14	0.003
α_3	1.9852	0.3492	57	5.69	<0.001
β_1	-0.0989	0.1555	57	-0.64	0.527
β_2	-0.0960	0.0442	57	-2.17	0.034
β_3	-0.0545	0.0278	57	-1.96	0.055
γ_1	-0.1692	0.0343	57	-4.94	<0.001
γ_2	0.1000	0.1201	57	0.83	0.409
γ_3	-0.3425	0.1281	57	-2.67	0.010
δ_1	-0.1382	0.0256	57	-5.40	<0.001
δ_2	-0.2559	0.0871	57	-2.94	0.005
δ_3	-0.1123	0.0215	57	-5.22	<0.001
λ	-0.6390	0.1136	57	-5.62	<0.001
μ_1	16.3750	0.3871	57	42.30	<0.001
μ_2	31.9969	4.3007	57	7.44	<0.001
μ_3	17.7550	0.5837	57	30.42	<0.001
σ^2_1	64.7046	7.5925	57	8.52	<0.001
σ^2_2	210.3400	64.1181	57	3.28	0.002
σ^2_3	67.4487	9.8537	57	6.84	<0.001
σ^2_{ui}	0.1731	0.0666	57	2.60	0.012

Table 5. Goodness-of-fit statistics calculated for different levels of grouping. $\hat{E}$: estimated mean error; P-Values calculated under the null hypothesis $H_0: E = 0$; $\widehat{RMSE}$: estimated root mean square error; $\widehat{MEF}$: estimated modelling efficiency; n: Amount of girth increment observations by level of grouping; Pp: *P. pinea*; Qi: *Q. ilex* subsp. *ballota*; Jt: *J. thurifera*; LDP: low density plot; HDP: high density plot. Period evaluated May 2012 to April 2015.

Scale	Level of grouping	$\hat{E}$	P-Value	$\widehat{RMSE}$	$\widehat{MEF}$	n
Whole		0.0092	0.445	0.694	33.4%	3306
Species	Pp	0.0320	0.267	0.997	25.1%	1197
	Qi	0.0023	0.865	0.363	39.2%	741
	Jt	-0.0069	0.588	0.473	37.5%	1368
Plot	LDP	0.0341	0.114	0.876	25.6%	1653
	HDP	-0.0156	0.153	0.444	49.8%	1653
Plot x Species	Pp – LDP	0.1128	0.064	1.379	11.7%	513
	Qi – LDP	0.0083	0.668	0.414	38.6%	456
	Jt – LDP	-0.0078	0.715	0.559	30.7%	684
	Pp – HDP	-0.0286	0.181	0.559	47.4%	684
	Qi – HDP	-0.0074	0.633	0.262	35.4%	285
	Jt – HDP	-0.0060	0.668	0.368	47.0%	684

Table 6. Goodness-of-fit statistics over the cumulative girth increment for the 58 trees studied. $\hat{E}$: estimated mean error; P-Values calculated under the null hypothesis $H_0: E = 0$; $\widehat{RMSE}$: estimated root mean square error; $\widehat{MEF}$: estimated modelling efficiency; n: number of trees. Period evaluated May 2012 to April 2015.

Scale	Level	$\hat{E}$	P-Value	$\widehat{RMSE}$	$\widehat{MEF}$	n
Whole		0.5351	0.386	4.653	92.6%	58
Species	<i>P. pinea</i>	1.8369	0.183	6.235	85.5%	21
	<i>Q. ilex</i>	0.1356	0.770	1.575	93.8%	13
	<i>J. thurifera</i>	-0.3876	0.655	4.119	96.2%	24
Plot	Low density	1.9529	0.076	5.929	90.8%	29
	High density	-0.8827	0.096	2.853	93.3%	29

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Table 7. Summary of model validation with annual radial increment data. n: number of trees sampled for the validation, n-sig: number of trees with a significant positive correlation between observed annual radial increment (obtained from cores and cross section slices) and predicted annual girth increment (obtained through the model); Ave-r: average value of the Pearson's correlation coefficient for the observed significant correlation; Max-r: maximum value of the Pearson's correlation coefficient. Validation time period: 1997-2011.

Species	Low density plot				High density plot			
	n	n-sig	Ave-r	Max-r	n	n-sig	Ave-r	Max-r
<i>P. pinea</i>	24	23	0.4007	0.6262	24	22	0.4761	0.6721
<i>Q. ilex</i>	2	1	0.4111	0.4111	2	2	0.4000	0.5736
<i>J. thurifera</i>	7	7	0.5497	0.7474	8	8	0.4248	0.6827

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Figure captions

Fig. 1. Average trajectories for the observed (solid lines) and predicted (dashed lines) girth increment values for the three species involved (Pp – *P. pinea*, Qi – *Q. ilex*, Jt – *J. thurifera*).

a) High density plot. b) Low density plot.

Fig. 2. Effects on secondary growth of the different covariates included in the definitive model. a) Optimum daily average temperature with different thermal amplitudes by species. b) Drought effect simulation considering initial water reserve (WR_0) = 0 and a single precipitation event on the first day of the simulation, where $P_1 = 5\text{mm}$.

Fig. 3. Observed vs. predicted cumulative girth increment values of individual trees shown by species at the end of the study period (1 062 days). a) *P. pinea*. b) *Q. ilex*. c) *J. thurifera*. Solid lines refer to the 1:1 line. Remarked are those *P. pinea* trees responsible for the bias in the low density plot. LDP: low density plot; HDP: high density plot.

Fig. 4. Observed values of annual radial increment (solid lines) vs predicted values of girth increment (dashed lines) for the randomly selected a) tree 1018 (*P. pinea*, low density plot), b) tree 1813 (*Q. ilex*, high density plot) and c) tree 1115 (*J. thurifera*, low density plot).

Fig. 5. Cumulative girth increment by species during the main growth period under current climate conditions (2014) and future climate forecasts (2075). 2075 growth projections calculated with an increment of 4.5 °C on average temperature, and a decrement of 30% in annual rainfall (climate model ACCESS I-0).

Fig. 1a. **Fig. 1b.**

Fig. 2a.

Fig. 2b.

Fig. 3a. **Fig. 3b.**

Fig. 3c.

Fig. 4a. **Fig. 4b.**

Fig. 4c.

Fig. 5

1 **Appendix. Distance dependent competition indices**

2 We used the distance dependent competition indices developed by Bella (1971) and later modified by
3 Tomé and Burhart (1989) to define intraspecific and interspecific interactions between the trees of the
4 area of study. They are area overlap indices (AOI) which calculate an influence zone around each
5 subject tree (ZA_i), where ZA_i dimension is related to tree size:

6
$$AOI_i = \sum_{j=1}^n \frac{ZO_{iq}}{ZA_i} \cdot \left(\frac{dbh_q}{dbh_i} \right)^k \tag{8}$$

7 These competition indices sum over all tree contestants for a subject tree i (n , being the number of tree
8 competitors whose area of influence intersects that of the subject tree i) the proportion of ZA_i that is
9 included in the influence zone of each competitor (ZO_{iq}). These proportions are weighed by the
10 term $\left(\frac{dbh_q}{dbh_i} \right)^k$, where dbh_i and dbh_q are diameter at breast height of the subject tree i and of the
11 competitor tree q respectively; k is a power factor. Among the different possible combinations
12 between k and radius of influence zone area for each species, R , we selected R equal to 30 times dbh
13 for intraspecific competition and 40 times dbh for interspecific competition. Concerning the weighting
14 factor k , we set $k=1$ for intraspecific interactions, indicating asymmetry on competition, and $k=0$ for
15 interspecific interactions, pointing to symmetric effects between species. This AOI combination has
16 already proved to accurately describe the effect of competition on growth in these *Pinus pinea*
17 admixtures in previous studies of the group. For more information on the use of this family of indices
18 in mixtures see de-Dios-García et al. (2015).

19

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