Disentangling the effects of competition and climate on individual tree growth: A retrospective and dynamic approach in Scots pine

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ABSTRACT

Understanding the relative contributions of competition and climate on individual tree growth is critical to project realistic forest dynamics under projected climate scenarios. Furthermore, present competition levels may reflect legacies of past use. Here, we analyze the effects of climate, site conditions and competition on radial growth in three Scots pine stands located along an altitudinal gradient in central Spain. Current stand structure and retrospective analyses of radial growth (basal area increment, BAI) were used to model changes in tree growth as a function of a spatially-explicit competition index (CI) and climate. Linear mixed-effects models were employed to model BAI and to quantify the growth responses to climate of trees under low and high competition levels. Competition effects on growth were steady over time regardless of tree age. High competition levels negatively affected growth since negative exponential functions characterized the CI–BAI relationships. Tree growth sensitivity to climate increased with decreasing competition intensity. Growth at high elevations was mainly limited by low winter temperatures, whereas warm spring enhanced growth at middle elevations and warm late summer temperatures constrained growth at low elevation. Growth responsiveness to climate is enhanced under low competition levels. Overall, current competition is a more relevant driver of recent growth than climate. Proactive forest management should be adopted to reduce the vulnerability of Scots pine forests currently subjected to higher competition levels and warmer and drier conditions.

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1. Introduction

Competition is a key process driving forest dynamics (Coomes and Allen, 2007; Kunstler et al., 2011). Trees of different sizes and canopy status compete differently for water and light (Orwig and Abrams, 1997), particularly when growth becomes limited by these resources (Tilman, 1988). Thus, trees may have different growth responses to climate, depending on the stand structural attributes (Andersen et al., 2008). It is known that changes in stand structure, climate and local site conditions alter tree growth and, as a result, forest dynamics (Lebourgeois et al., 2014). Thus, the

growth rates of neighboring trees may vary markedly across monospecific forests with contrasting ages and structures (e.g., Hara, 1984; He and Duncan, 2000). This variation in growth rates in turn influences stand dynamics, driving size structure and spatial pattern diversification (Gómez-Aparicio and Canham, 2008; Castagneri et al., 2012; Fraver et al., 2014). Understanding the relative contributions of stand structure and climate on growth should be essential to achieve accurately estimations of forest dynamics, as well as to assess forest vulnerability under a climate change scenario (Lindner et al., 2010).

Past forest dynamics, including disturbances and management, affects current individual tree growth responses to climate through legacies determining present stand structure (Farrell et al., 2000; Rozas, 2014). Accordingly, competition has usually been characterized at the stand or plot levels through summary indicators such as density or basal area. However, competition and climate–growth sensitivity are tree-level processes that should be explicitly taken into account at the individual scale where selection operates (Carrer, 2011; Rozas, 2014). In addition, the specific case of long-living organisms such as trees, the social status and climate sensitivity demand a representative time span (Lebourgeois et al., 2014).

During the last decade, numerous studies have highlighted how competition interacts with growth responses to climate in different tree species and forest biomes (e.g., Weber et al., 2008; Ruiz-Benito et al., 2013; Madrigal-González and Zavala, 2014). Competition for nutrients, water and light is known to limit tree growth, and this effect has been estimated using competition indices (Daniels et al., 1986; Holmes and Read, 1991; Biging and Dobbertin, 1992; Kunstler et al., 2011). For instance, contrasting responses to climate between dominant and suppressed trees have been frequently reported within the same stand (Cherubini et al., 1998; Castagneri et al., 2008; Linares et al., 2010). However, tree competition estimates usually provide only a static picture based on the current stand structure (Burton, 1993), while dynamic competition estimates and related climate–growth responses remain poorly understood (but see Weber et al., 2008; Dorman et al., 2015). We argue that this temporal component of competition is supported by at least two aspects influencing tree growth. First, competition depends on the phenotypic plasticity of crown and root systems over time, which influences the access to resources such as light, water and soil nutrients (García, 2014). Second, the uses of these resources also determine how competition proceeds through time. For instance, in drought-prone areas trees compete for water, thus reducing the amount of water available for their neighbors. Following this rationale, those trees able to cope with intense drought stress might maintain higher growth rates, inhibiting growth of neighboring trees through shading (Craine and Dybzinski, 2013).

Tree-ring data provide individual- and time-explicit information of competition by reconstructing growth patterns of individual trees (Weber et al., 2008; Pach and Soberka, 2011), and by quantifying the effects of climate and competition on these growth patterns (Cook, 1990). The competitive status of individual trees is affected not only by past growth changes (e.g., suppressions or releases), but also by precedent mean growth rates (Banks, 1991). The century-long exploitation of European forests further complicates the inference of past competition in these stands through the reconstruction of radial growth (Fritts, 2001). The massive migration of rural populations in Europe over the past century has favored forest encroachment. Nonetheless, the current stand structures still reflect the legacy of past human activities (Barbero et al., 1990; Chauchard et al., 2007; Gimmi et al., 2010).

The present paper addresses these issues by reconstructing and quantifying the competitive dynamics of three Scots pine (*Pinus sylvestris* L.) stands subjected to different climatic limitations along an altitudinal gradient located in central Spain (Sánchez-Salguero et al., 2015). The stands are located in a formerly logged area which has not been intensively managed since the 1980s (Gea-Izquierdo et al., 2014). Our aim was to analyze how past forest management determines current tree-to-tree competition using growth data and assessing sensitivity of tree growth to climate. We hypothesize that the role played by regional climate as a growth constrain is modulated by the competitive conditions among neighboring trees. Specifically, we expect that trees subjected to high competition are more sensitive to drought stress, particularly at low-elevation sites.

2. Material and methods

2.1. Study area

The study was carried out along an altitudinal gradient located on the north-facing slopes of the Spanish Central Range (Valsaín Forest, Sierra de Guadarrama National Park; 40°49′N, 4°01′W, altitudinal range 1100–2125 m a.s.l.). The forest is dominated by Scots pine (*Pinus sylvestris* L.), although other tree species occur in marginal areas of the forest (*Quercus pyrenaica* Willd., *Quercus ilex* L., *Pinus nigra* Arn.). This area is located near the southernmost limits of the distribution of Scots pine. Climate is Mediterranean with marked continental influence, characterized by dry summers and cool winters (Appendix A, Fig. A1). The total annual rainfall is 1266 mm and the mean annual temperature 6.5 °C (at 1890 m a.s.l.), with December–January (mean temperature of −0.4 °C) and July–August (mean temperature of 16.5 °C) being the coldest and warmest months, respectively. The bedrock is mainly formed by granite and gneiss. Soils are shallow and usually acid being predominantly humic cambisols and leptosols at high-elevation sites (Forteza et al., 1988).

In this study, we used monthly climate data (mean, maximum, minimum temperatures and total precipitation) for the period 1985–2011, obtained from three meteorological stations located near the study sites at different elevations: Puerto de Navacerrada (40°47′N, 4°00′W, 1894 m a.s.l.), Granja de San Ildefonso (40°46′N, 4°00′W, 1191 m a.s.l.), and Segovia (40°56′N, 4°10′W, 1005 m a.s.l) and additional climatic data measured within forests (see Sánchez-Salguero et al., 2015 for details). Data were provided by the Spanish National Meteorological Agency (AEMET).

Historical evidence and dendrochronological studies show that the Valsaín forest has been intensively managed for centuries (Donés and Cabrera, 2009; Génova, 2012). The forest has been dedicated to timber production with an established management plan since 1889 (Rojo and Montero, 1996). This even-aged forest has been managed from group shelterwood system (rotation of 140 years and regeneration period of 40 years) to selective cuttings (Barbeito et al., 2011), which have been reduced in intensity and frequency until the 1980s, when a forest reserve was established. A flexible management plan was then introduced to increase the priority of recreational activities and biodiversity conservation (Montes et al., 2005).

2.2. Field sampling

In August 2012, field sampling was carried out in three Scots pine stands located at different elevations (Table 1, Fig. 1; additional information on the study area is available in Touchan et al., 2013). Since we were mainly interested on individual tree growth than on stand patterns, we chose to sample more intensively all trees located within each plot than to replicate several plots at each of the three elevations. Therefore, one square plot (40 m × 40 m) per elevation was randomly located at 1400 m near

the lower limit of the distribution of Scots pine (henceforth the low-elevation plot), at 1650 m (the mid-elevation plot) and at 1900 m near the uppermost forest limit (the high-elevation plot). All trees on each plot with a diameter at 1.3 m from the base (dbh) greater than 7.5 cm were identified, tagged and mapped and their dbh and height were measured (Table 1, Fig. 1).

All sampled trees were cored at 1.3 m using increment borers, and two cores per tree were extracted along the contour line. The cores were air dried, sanded until tree rings were clearly visible and the tree rings were visually cross-dated. Individual tree-ring width series were measured to the nearest 0.01 mm using a LINTAB semi-automatic measuring device (Rinntech, Heidelberg, Germany). Cross-dating quality was checked using COFECHA (Holmes, 1983). Tree age at coring height (cambial age) was estimated for each individual based on the core with the higher number of tree rings (including the number of missed rings between pith and first tree ring). The size-related growth trend, which is due to the geometrical constraint of an increasing volume of wood with increasing stem diameter, was corrected by converting the tree ring widths into basal area increments (hereafter abbreviated as BAI). This is a more biologically meaningful descriptor of growth trends than only tree-ring widths (Biondi and Qaedan, 2008). The BAI was calculated from tree-ring widths as the difference between consecutive basal areas using the equation BAI = π $(R^2_t - R^2_{t-1})$, where R is the radius of the tree and t is the year of tree-ring formation.

2.3. Dynamic competition index

We estimated the between-tree competition index (CI) for each focal tree by calculating a distance-dependent competition index at an individual scale for each year, taking into account the number and size of the neighboring competitors and their distance to the focal tree (Hegyi, 1974):

$$CI = \sum_{j}(dbh_j/dbh_i)/dist_{ij} \qquad (1)$$

The competition index (CI) of focal tree i was calculated as the sum of the quotients dbh_j/dbh_i, obtained for all j neighboring trees located within a given radius R from the focal tree, divided by the distance between trees i and j ($dist_{ij}$). If a focal tree has zero competitors, the CI takes a value of 0. The CI calculation was based on the assumption that a high dbh value implies also a high competitiveness of a tree. Correspondingly, trees with a large dbh exert competitive stress on neighboring trees with lower dbh values. The threshold radius above which neighbors were regarded as not competing was estimated by comparing the BAI and CI for each plot considering radii of 2, 4, 6, 8, 10 and 12 m (Appendix A, Fig. A2). To correct the edge effect of CIs calculated for circles whose radii overlap the plot boundary we used an area-weighted

edge correction by dividing the CI by the proportion of the area of the circles that lay inside the plot for any given focal tree (Das, 2012). The mean BAI–CI relationship was calculated for the same period 1985–2011 since the last harvest occurred before the early 1980s (Barbeito et al., 2011). The period was thus long enough to detect changes in the competitive relationships and the BAI responses to climate, but short enough to detect indirect evidence of past management such as stumps (Weber et al., 2008).

The highest correlations between CI and BAI were obtained for a plot radius of 8 m, and this was used in further calculations. Finally, we derived a retrospective CI using diameter data calculated from annual tree rings to analyze the changes and trends in the CI values (Pach and Soberka, 2011).

2.4. Unraveling the effects of competition and elevation on BAI

To define the social statuses of the trees we fitted exponential-decay functions between the CI and BAI using the approach previously elaborated by Linares et al. (2010). We assumed that a CI equal to zero indicates potential site productivity, i.e. it is the expected BAI value when no competitors affect tree growth. We then selected the CI corresponding to 50% of the BAI reduction as it is related to the potential site productivity. Finally, this value was determined for a CI = 2.5 using the whole dataset, i.e. considering all trees sampled in the three plots. Then, we separately analyzed trees with low competition intensity (abbreviated as LC trees) defined as those with CI < 2.5, and trees with high competition intensity (abbreviated as HC) which were considered those with CI ⩾ 2.5 (Appendix A, Fig. A3). We also tested the cumulative effects of competition on BAI by including previous-year competition in the calculations (Weber et al., 2008). Trends in BAI and CI over time were explored by plotting five-year cumulative BAI values over five equal periods, considering the time spans 1986–1990, 1991–1995, 1996–2000, 2001–2005 and 2006–2010. We performed repeated-measures ANOVAs to reveal any differences in competitive dynamics between trees.

2.5. Linear mixed-effects models: BAI residuals as a function of climate

The BAI variance that could not be explained by the competition index, i.e., the residual error from the exponential-decay models of BAI–CI, was modeled as a function of climate using linear mixed-effect models of the form:

$$Y_i = Xa_i + Zb + e_i \qquad (2)$$

where Y_i represents BAI residuals in year i, a is the vector of fixed effects (i.e., estimated for the climatic variables for each year), b is the vector of random effects corresponding to the tree identity, X and Z are regression matrices, predictor variables and variables used to calculate the random effects (i.e., intercept), respectively,

Table 1
Summary of the main tree characteristics measured in the three Scots pine plots located at different elevations. The number of measured trees and radii are presented for all trees, and also for high- (HC) and low-competition (LC) trees, separately. Different letters indicate significant ($P < 0.05$) differences between the plots (one-way ANOVA test).

Plot		Dbh (cm)	Height (m)	Age at 1.3 m (years)	Basal area (m² ha⁻¹)	Density (tree ha⁻¹)	No. trees (radii) (No. LC/HC trees)
Low-elevation	Maximum	53.7	21.5	130	17.7	520	83 (142)
	Mean	34.3b	16.5b	84b			55/28
	Minimum	7.5	3	47			
Mid-elevation	Maximum	68.5	22	209	13.9	715	115 (176)
	Mean	31.7a	13.9a	72a			71/44
	Minimum	7.5	3	44			
High-elevation	Maximum	62.7	28.1	190	21.7	480	76 (90)
	Mean	40.7c	17.8c	127c			46/30
	Minimum	7.5	3	34			

and e_i is the within-group error vector. Models were fitted for all trees on each plot and separately for the LC and HC trees.

Following a stepwise procedure, residuals not explained by the CI model (step 1) or the climate model (step 2) were considered to be autocorrelation effects. These modeling steps were performed independently of the climate–growth model, and it was assumed that climate data can have some autocorrelation, which should be included as climate effects. The BAI of the previous year (BAI$_p$) was introduced into the model as an additional fixed effect to account for the first-order temporal autocorrelation of this variable instead of calculating autoregressive parameters; because this reflects in a more realistic way the effects of the prior growth rate on the current growth. Using the same stepwise procedure, we analyzed the residuals from the last model versus cambial age to

account for potential age effects. Finally, the residuals of the models were checked graphically for normality, homoscedasticity, and presence of autocorrelation. All the previous models were compared with a null model, which considered the BAI or the residuals of the previous models to be a constant (see Biondi and Qaedan, 2008). The random effects and the covariance parameters were estimated using the restricted maximum-likelihood method (Zuur et al., 2009). We used an information-theoretic approach for multi-model selection (see Burnham and Anderson, 2002), based on the Akaike Information Criterion corrected for small sample sizes (AICc). The AICc combines the measure of goodness of fit with a penalty term based on the number of parameters (k) used in the model, i.e., it selects the most parsimonious models. We also calculated Δi, which is the difference in AICc with respect to the
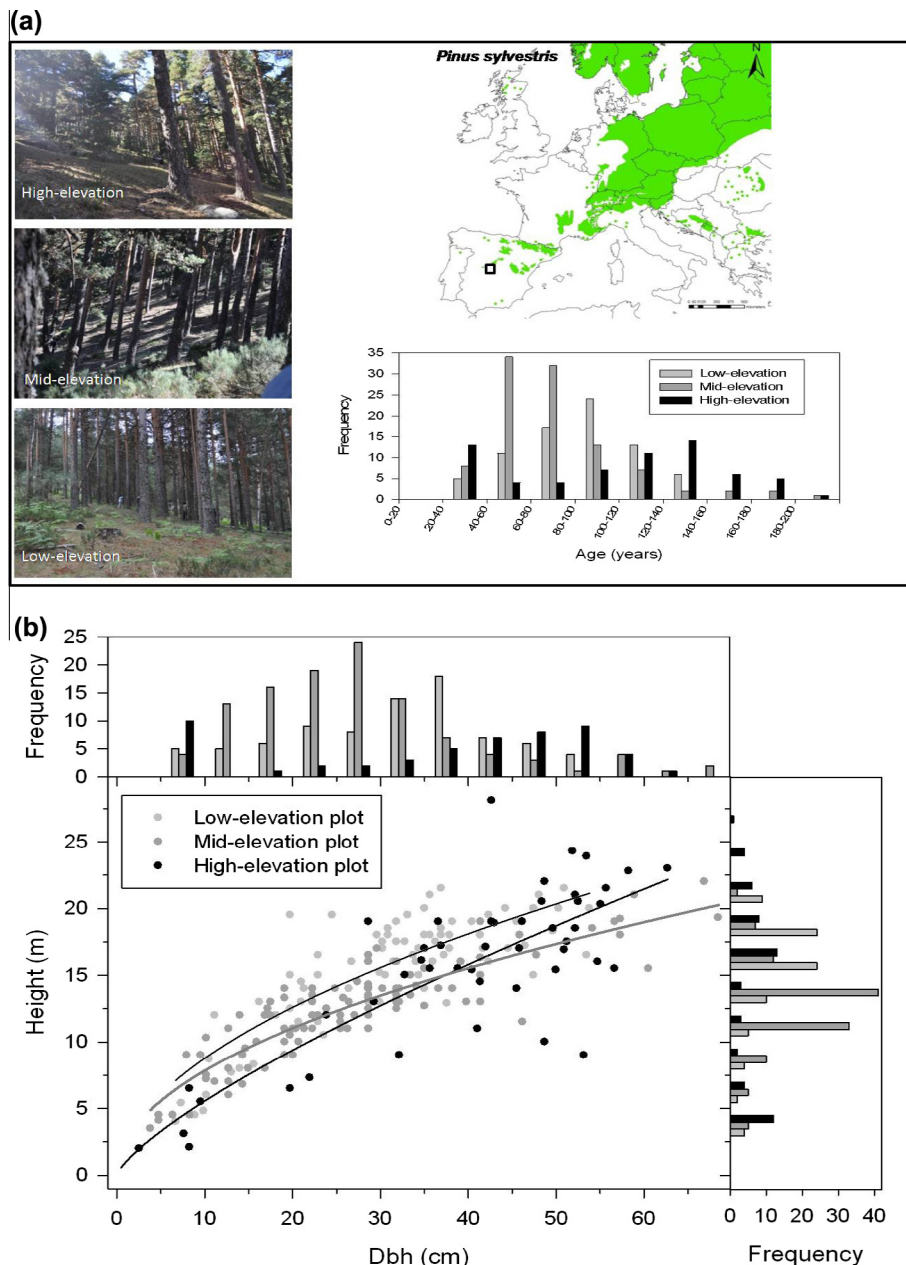

Fig. 1. Distribution of Scots pine in Europe (EUFORGEN, 2009; www.euforgen.org) and location of the study site (black square) in Central Spain with views of the three study sites and corresponding age histograms (a). Associations between size data structure (Dbh, diameter at breast height; Height) and the frequency of sampled trees on each plot (b).
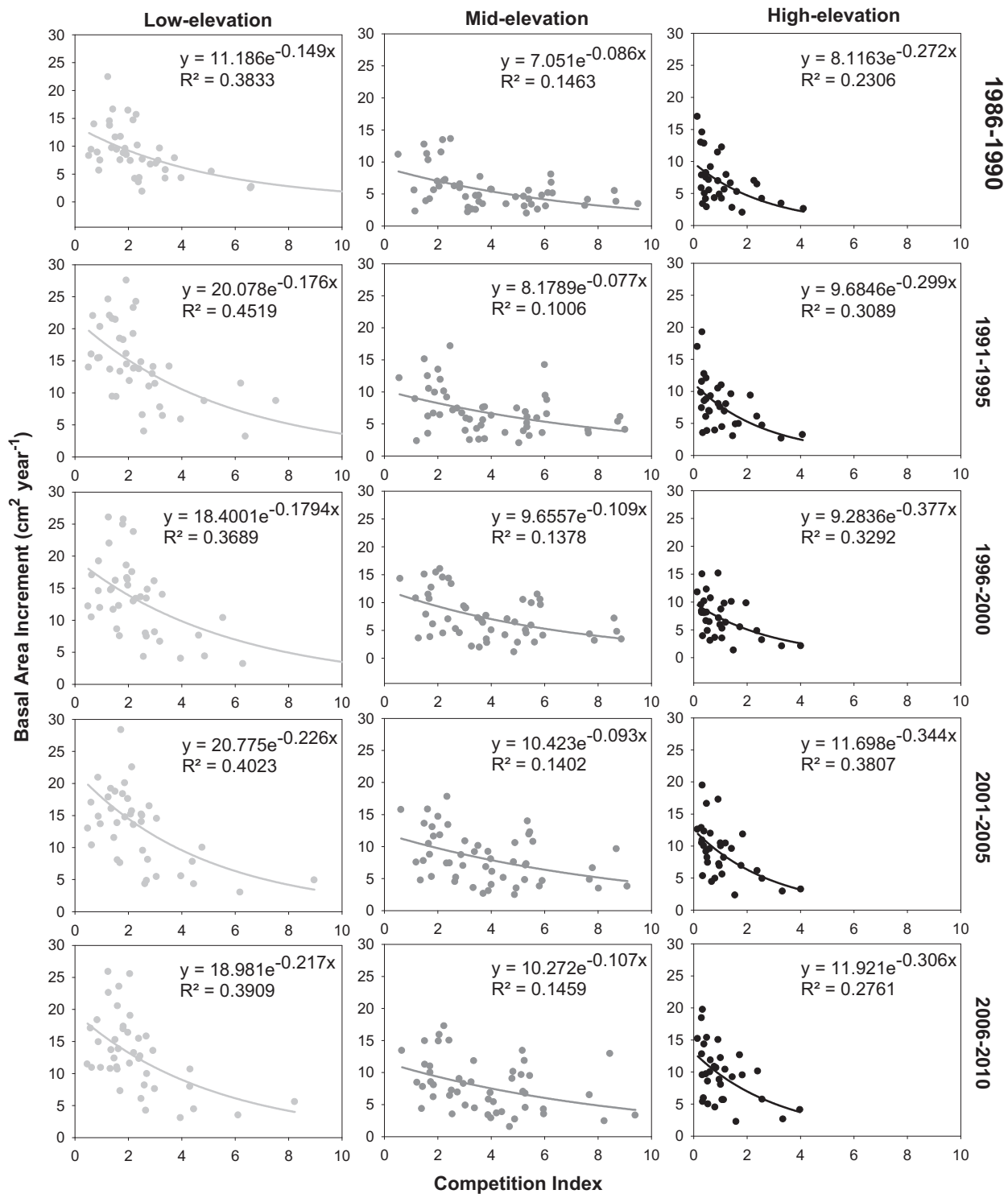
Fig. 2. Relationships between the competition index and the basal area increment of trees in the low- mid- and high-elevation study plots for the five time periods 1986–1990, 1991–1995, 1996–2000, 2001–2005 and 2006–2010. A subset of the total number of trees was used because of edge effects. The negative-exponential functions for each plot are represented with different symbol shades and lines (gray, low-elevation; dark gray, mid-elevation and black, high-elevation). The regression parameters are based on the negative exponential functions ($y = ae^{-bx}$) between radial growth (the dependent variable, expressed as a mean basal area increment for the analyzed period, BAI) and the competition index (the independent variable), for different time periods. Probability levels for the regressions were significant at $P < 0.001$ in all cases.

best-fitting model, and the Akaike weights Wi (i.e. the relative probability that model i would be the best-fitting model for the observed data). We considered models with substantial support to be those in which the Δi was less than 2 (Zuur et al., 2009).

We fitted linear mixed-effects models using the *nlme* library of the R statistical software version 3.1.2 (R Development Core Team, 2014). All data are presented with mean ± standard errors.
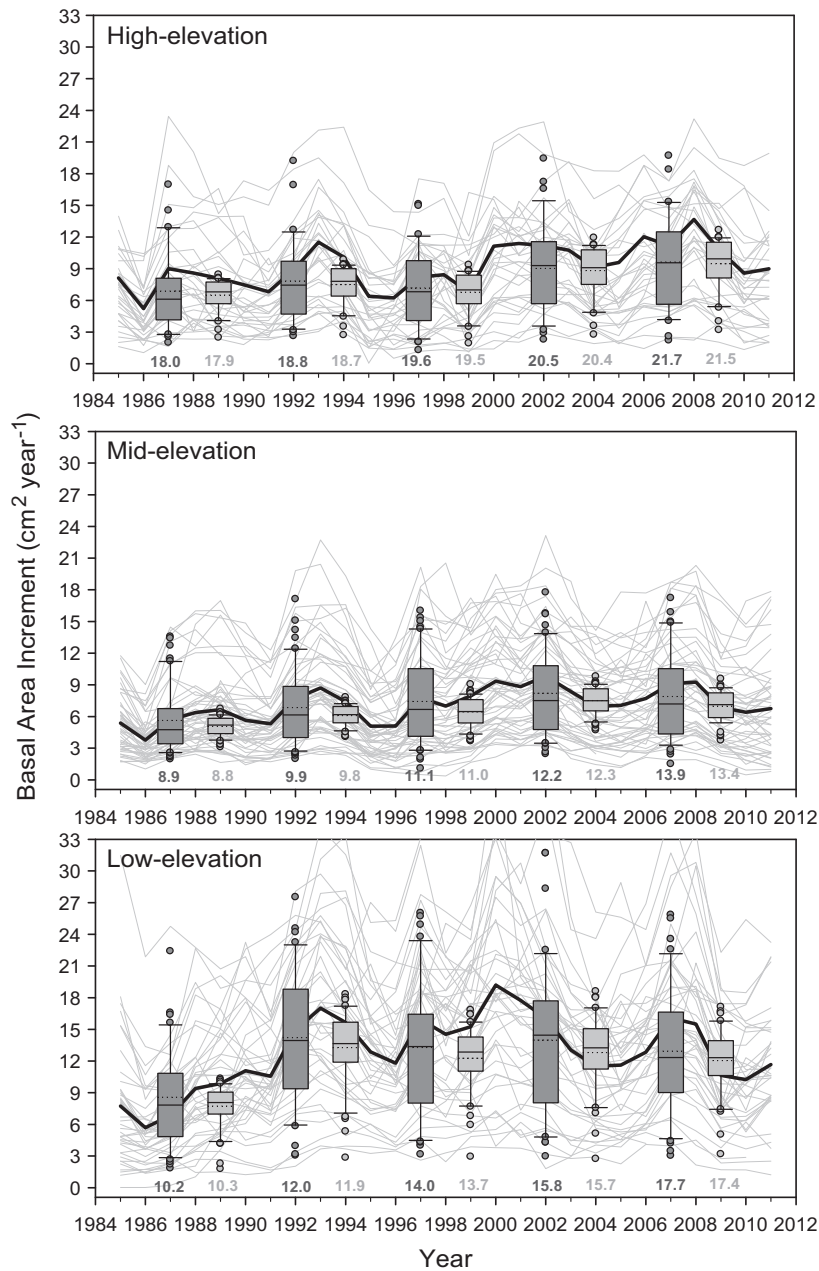
Fig. 3. Basal area increment (BAI) considering all trees (gray lines) and average BAI (black line) of each Scots pine plot for the period 1985–2011. Box-plots represent the average 5-year periods for the observed (dark gray) and fitted (gray) BAI values for the five periods 1986–1990, 1991–1995, 1996–2000, 2001–2005 and 2006–2010, based on dynamic competition models (see Fig. 2). The value of the observed (dark gray) and fitted (gray) stand basal area (BA, m^2 ha^{-1}) for each period is indicated under each box plot as a numbers. Error bars represent the 5th and 95th percentiles, boxes the standard errors, solid lines the median, dashed lines the mean and circles the outliers. Differences between the observed and fitted values were not significant (ANOVAs, $P > 0.05$).

3. Results

3.1. Size and age structures

Trees from the high-elevation plot were older and presenter larger diameters and tree heights than those located in the other two sites, whereas trees sampled in the mid-elevation plot were the smallest (Table 1, Fig. 1). The tree densities in the three plots did not differ significantly ($P = 0.15$), despite the three sites showed contrasting stand structures (Fig. 1).

3.2. Growth and competition dynamics

The reconstructed CI values did not change during the period 1985–2011 (Appendix A, Fig. A4). Low BAIs were associated with increasingly high between-tree competition over time in the three plots (Fig. 2). Considering the entire study period, all plots showed significant negative exponential relationships between CI and BAI, and this association accounted for 14–45% of the BAI variance (Fig. 2). The weakest CI–BAI association was found in the mid-elevation site.

Table 2

Statistical parameters used in the models of the basal area increment (BAI). Their partial variance is explained. Models are based on: the competition index (CI), climate variables (see Table 3) and the BAI of the previous year (BAI$_p$). Parameters are presented for all trees in each study site, and considering the low- (LC) and high-competition (HC) trees, separately.

Model	Low-elevation plot	Mid-elevation plot	High-elevation plot	LC trees	HC trees
CI	30.42	11.53	23.64	10.49	30.29
Climate	34.82	60.79	48.30	56.96	28.08
BAI$_p$	10.96	7.53	4.50	9.07	10.36
Variance (%)	76.19	79.85	76.43	76.52	68.74
Residuals error	23.81	20.15	23.57	23.48	31.26
No. trees	82	110	76	169	99

The model relating BAI and CI was calculated for five 5-year long sub-periods for the 1985–2011 period (Fig. 3). The selected models for each period were based on exponential-decay functions explaining the average BAI for 5-year periods (Fig. 2). These single CI models appeared to fit the BAI data for each period and plot reasonably well (Fig. 3). Trees showing higher CI also presented lower mean BAI values regardless of the period considered (Figs. 2 and 3). The BAI–CI relationships in the periods 1991–1995 and 1996–2000 were similar, although precipitation was low from 1991–1995 and high from 1996–2000 (Fig. 2; see also Appendix A, Fig. A1). Variations in the mean annual precipitation and temperatures determined the strength of the BAI–CI relationship. The variance explained by the competition thus increased slightly during drought periods (1991–1995) at low elevations compared to the fitted BAI–CI models (Fig. 2) and the climate data (Appendix A, Fig. A1). Overall, LC trees were characterized by mean BAI values above the 7 cm^2 year^{-1} threshold and HC trees by values below that threshold (see Appendix A, Fig. A3).

Comparing the variance explained by each of the models of CI effects (step 1), climate effects (step 2) and autocorrelation structure (step 3) for the three plots reveals the relative influence of the stand structure, climate and growth autocorrelation on tree growth dynamics (Table 2). The climate model accounted generally for more of the explained variance (Table 2), while the autocorrelation model explained less of the variance. More BAI variance was explained by climate in the mid- than in the high- and low-elevation plots. However, competition and autocorrelation effects explained less BAI variance at the low-elevation plot.

3.3. Linear mixed-models of BAI variance non-explained by stand structure

Climatic conditions were extremely variable during the study period, with relatively rainy periods (1996–1998, 2000) alternating with severe droughts and warm periods (1993–1995, 1999, 2005; see Appendix A, Fig. A1). The best-fitting climate-based model of BAI included January temperature (positive correlation), with increasing amounts of variance explained at the high-elevation plot (Table 3, Appendix A, Table A1), February temperature (positive correlation) for low- and mid-elevation plots, and March temperature for the high-elevation plot. High late-summer temperatures, usually associated with low water availability, negatively affected BAI in the low-elevation plot, and explained about 25% of the BAI variance, while spring precipitation had a positive effect (accounting for 13% of the BAI variance) on BAI in the high-elevation plot (Table 3). Although summer precipitation had a positive effect on BAI in the mid-elevation plot, it explained less of the BAI variance (only 7%) than late summer or fall precipitation in the mid- and high-elevation plots (Table 3). Tree age seemed to have no significant effect on these climate-based models of BAI.

The selected BAI models based on CI, climate and BAI$_p$ explained the observed BAI reasonably well, accounting for 76%, 80% and 76% of the BAI variance in the low-, mid- and high-elevation plots, respectively (Fig. 4, Appendix A, Fig. A5 and Table A2). Over time, LC trees showed a slightly higher cumulative basal area (BA) than HC trees (Fig. 4). The LC trees responded stronger to climatic conditions in their BAI patterns since 57% of the BAI variance was explained by climatic variables, whereas only 4–11% of the BAI variance was explained by BAI$_p$ (Table 2).

The final BAI model applied to HC trees explained 69% of the variance (Table 2). Years with lower BAI values coincided for the LC and HC trees, but the absolute growth of the LC trees however, declined more during dry periods than that of the HC trees. The growth increases in the LC trees were also higher than in the HC trees (repeated-measures ANOVA, $F = 14.4$, $P < 0.05$). Climate effects were significantly related to the residuals of the CI–BAI model for the HC trees, while LC trees showed no significant trends (results not shown). The relative weight in the model and the explained BAI variance of CI-related fixed factors highlights again the effects of competition on growth (Appendix A, Table A2). High CIs more negatively affected BAI in HC tree than in the case of LC trees (Table 2). Moreover, the degree to which BAI responded to climate was inversely related to the CI (Table 2).

4. Discussion

Our findings support the hypothesis that growth constrains related to competition intensity and climatic stress interact through time. We detected significant legacies in current stand structure and competition dynamics. The competition dynamics (Fig. 2) and the growth patterns observed in the three study plots (Figs. 3 and 4) indicate that some trees have already entered the phase of growth stagnation (Oliver and Larson, 1996), probably due to competition for light and water, which could trigger

Table 3

Effects of climatic variables on basal area increment (BAI) based on linear mixed-effects models. The values are parameters and their associated standard errors (SE) and the variance explained (%). Positive (+) and negative (−) effects on BAI are indicated for the following climatic variables: maximum temperature (Tx) in January (1), February (2), March (3), September (9); and precipitation (P) in March (3), August (8) and October (10).

Climatic variables	Low-elevation plot			Mid-elevation plot			High-elevation plot		
	Value	SE	Variance (%)	Value	SE	Variance (%)	Value	SE	Variance (%)
Tx1	0.049	0.017	4.03	0.053	0.016	15.83	0.056	0.017	19.12
Tx2	0.047	0.017	5.29	0.019	0.014	9.50	–	–	–
Tx3	–	–	–	0.017	0.012	15.62	–	–	–
Tx9	−0.042	0.017	25.48	–	–	–	–	–	–
P3	–	–	–	–	–	–	0.001	0.017	12.93
P8	–	–	–	0.002	0.007	7.76	–	–	–
P10	–	–	–	0.001	0.017	12.08	0.001	0.017	16.26
Random effect	0.315	–	–	0.449	–	–	0.439	–	–
Residual random effect	0.388	–	–	0.325	–	–	0.345	–	–

increasing mortality rates (Bigler et al., 2006). Furthermore, our results support the hypothesis that climate sensitivity of individual tree growth is determined by competition between neighboring trees, providing a link between past forest dynamics, recent stand structure and current tree vulnerability to climate change.

The modulating effects of stand-structure components as the competition intensity on tree climate–growth sensitivity across ecological gradients are still not fully understood (but see Linares et al., 2010; Hartmann and Messier, 2011; Martín-Benito et al., 2011). Recent studies suggest that ecological conditions do not significantly affect the climate sensitivity of different forest types according to inventory data (e.g., Gómez-Aparicio et al., 2011; Ruiz-Benito et al., 2014). However, the retrospective dynamic competition index applied in our study provides an individual-based, spatial- and time-explicit approach, which allows us reconstructing stand-level competition dynamics over time. Furthermore, by taking into consideration both the magnitude and the trend in competition dynamics, we were able to assess tree-level competition

processes. This issue is relevant because competition among trees might cause much larger reductions in forests growth and carbon uptake than climate stress (Vayreda et al., 2012; Rozas, 2014).

In similar Iberian Scots pine forests, growth reduction observed as a consequence of enhanced tree-to-tree competition is mainly the legacy of past management as well as the effect of current abandonment of forestry practices (Montes et al., 2005; Fernández-de-Uña et al., 2015). The effects of canopy closure and subsequent stand stagnation coupled with above- and below-ground competition are reflected in the growth curves grouped according to their social status. Tree size modulates the direction and intensity of the competitive interaction, since large trees generally have more capacity to intercept solar radiation and acquire resources such as soil water and nutrients. However, dominant large trees may also be more vulnerable to climatic stresses such as drought than suppressed individuals (Thomas and Winner, 2002; Niinemets, 2010). Furthermore, strong competition reduces inter-annual growth variation, which is associated with lower
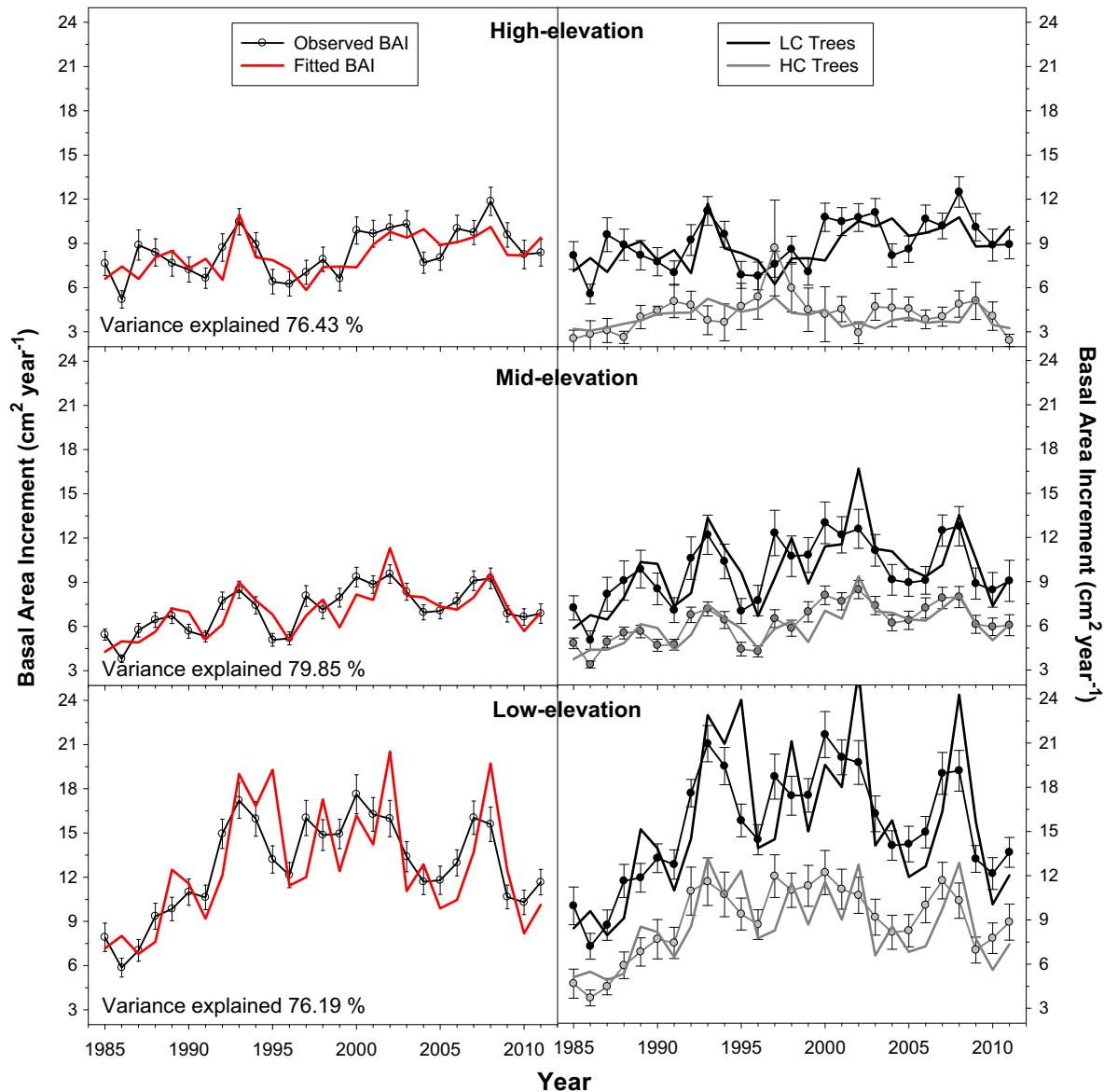

Fig. 4. Observed (thin lines with symbols) and fitted (thick lines) basal area increment data for all trees sampled in the three Scots pine stands (left-column plots) with the low-competition (LC) and high-competition (HC) trees considered separately (right-column plots). The inset displays the amount of variance explained by the fitted models for all trees. Error bars represent the standard errors of the mean.

growth sensitivity and a weak climatic response of smaller trees in high-competitive environments (Martín-Benito et al., 2011; Rozas and Olano, 2013). The finding that dominant trees are most sensitive to climate variations corresponds with that of previous studies, which focused on the climatic signal of tree populations according to size or social status (Mérian and Lebourgeois, 2011; Zang et al., 2012). We acknowledge that more replication at the stand level would be required to extrapolate our conclusions for broader spatial scales and ecological gradients. However, we emphasize that our analyses focused on trees and thus we decided intensifying our sampling effort at this scale for at least two reasons: (1) individual trees, neither forests nor stands, react to climate and competition (Galván et al., 2014); and (2) ecological inferences must be done at the correct scale of study to avoid incurring an ecological fallacy (Idrovo, 2011).

Our results illustrate how high-frequency growth changes are related to the climate along the ecological gradient, whereas mean growth (BAI) was reasonably well predicted by the competition intensity experienced by the trees. Although competition is able to reduce, cancel out or mask the climatic signal reflected in the growth patterns, climate warming negatively affects the growth and survival of trees subjected to strong competition in
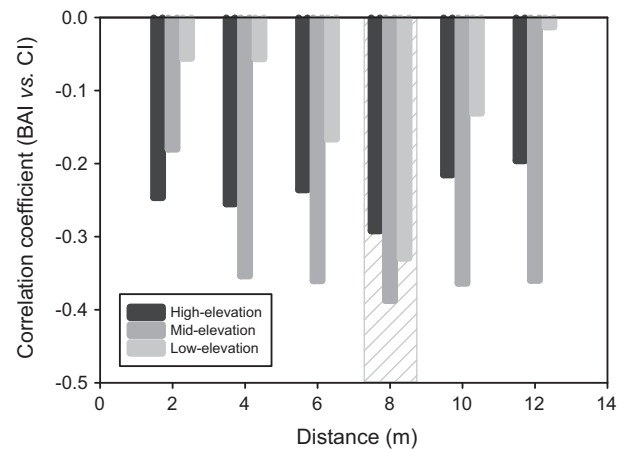

Fig. A2. Selection criteria for the distance from each focal tree used to calculate the competition index (CI) in the three Scots pine plots. The plot shows Pearson correlation coefficients calculated between the basal area increment (BAI) and the CI at several distances from the focal tree (2, 4, 6, 8, 10 and 12 m). The striped gray bar shows the distance selected for calculating the CI where correlations were the highest for the three study plots.
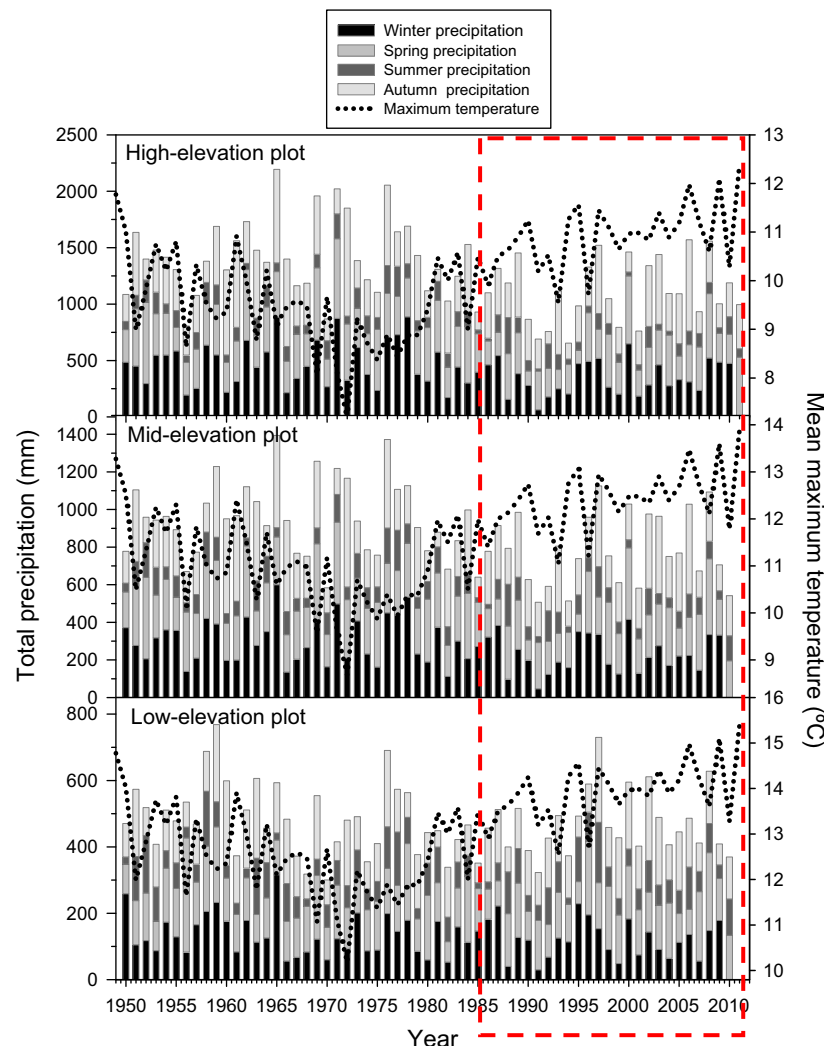

Fig. A1. Mean annual maximum temperature and seasonal precipitation patterns for the three Scots pine plots located at low, mid and high elevations (data correspond to the period 1950–2011). The dashed square highlights the study period with growth data.
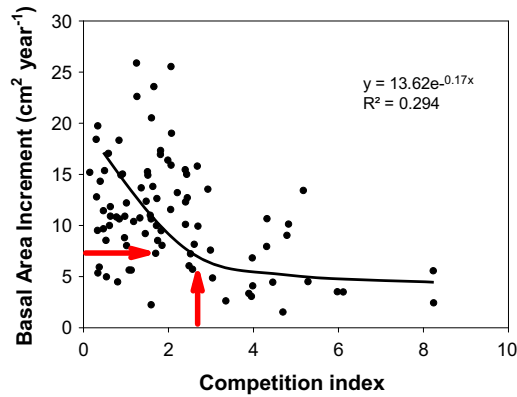
Fig. A3. Threshold for grouping low competition (LC) and high competition (HC) trees based on the dataset for the competition index (CI) and the basal area increment (BAI) for the three plots. The red arrows indicate 50% of growth reduction (BAI approx. 7.5 cm^2 yr^{-1}) related to the potential site productivity (CI approx. 2.5). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. A4. Reconstructed dynamic competition indices for the periods, where CI-85 are for the period 1986–1990; CI-90 for 1991–1995; CI-95 for 1996–2000; CI-00 for 2001–2005; and CI-05 for 2006–2010 (see Section 2). In the box plots, error bars represent the 5th and 95th percentiles, boxes the standard errors, solid lines the median, dashed lines the mean values, and dots the outliers. Differences between the periods for repeated measurements were not significant (ANOVAs, $P \geqslant 0.05$).

drought-prone areas (Linares et al., 2010; Rigling et al., 2013; Gea-Izquierdo et al., 2015). However, quantifying the effects of stand structure and climate on tree growth, and detecting changes in growth sensitivity to climate as illustrated here provides a more realistic picture of the vulnerability of individual trees to climate warming (Galván et al., 2014). Such findings can also provide the basis for guidelines on proactive management.

Individual radial growth responses to limiting climate factors, e. g. cold winter temperatures at high elevation and spring–summer aridity downslope, were influenced by competition. However, it should be taken into account that we modeled age effects assuming a linear relationship and the possibility of a non-linear relationship between BAI and age remains (Biondi and Qaedan, 2008; Fernández-de-Uña et al., 2015). This finding partially contradicts that of previous studies on Scots pine forests, which suggested that older trees are more sensitive to water availability than younger ones (Linderholm and Linderholm, 2004; Bogino et al., 2009; Bauwe et al., 2013), and that different size classes have similar growth responses to climate (Mérian and Lebourgeois, 2011; Zang et al., 2012). Covariation between tree size and age complicates the understanding of the factors underlying changes in tree growth (Mencuccini et al., 2005). The same limitation could be pointed out for competition, as larger and usually older trees are seldom subject to strong competition.

Larger trees tend to be more sensitive to drought than smaller trees (Mérian and Lebourgeois, 2011), which supports our first hypothesis that the sensitivity of tree growth to climate is driven by competition. On the other hand, specific elevation-related responses to climate were mainly detected for thermal constraints of growth. In the study area, Scots pine growth seems to be mainly limited by previous winter temperatures at higher elevations, and by current spring temperatures at mid elevations and by late summer temperatures at low elevations (see also Bigelow et al., 2014; Sánchez-Salguero et al., 2015). Trees growing in the low-elevation were surprisingly not more sensitive to precipitation than high-elevation trees (but see Candel-Pérez et al., 2012). This finding supports the claim that temperature plays a key role in the radial growth of Mediterranean trees under continental climate conditions (Camarero et al., 2010; Herrero et al., 2013; Sánchez-Salguero et al., 2015). Various suggestions have been made to explain this thermal restriction including specific features in the seasonal dynamics of carbohydrate storage and synthesis, cambial reactivation or leaf phenology (Gimeno et al., 2012). We also suggest that trees of different sizes are differently affected by microcli-
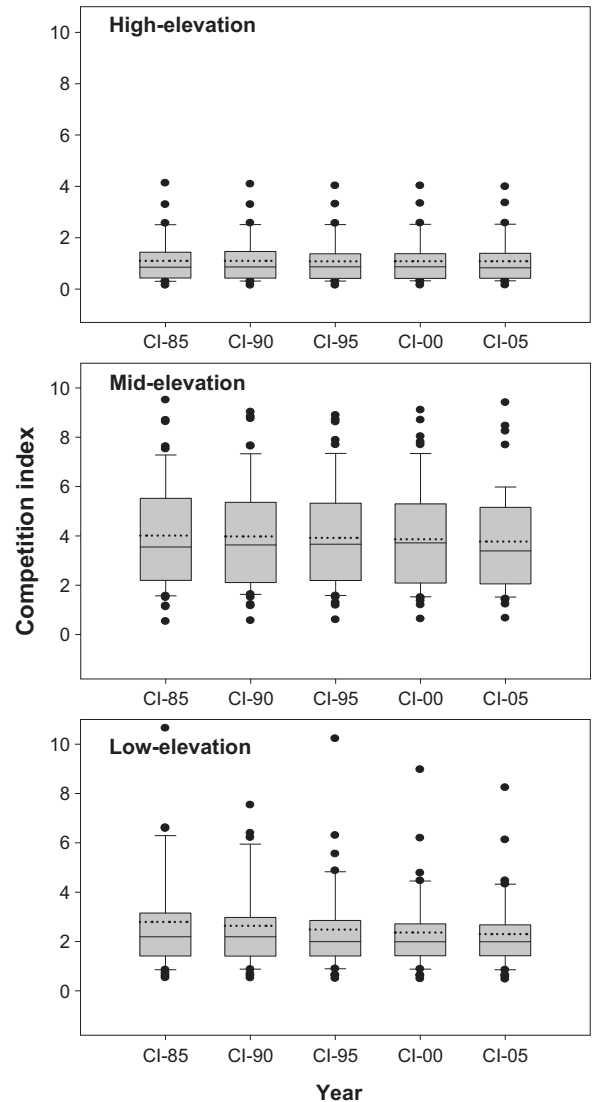
matic variations. Smaller trees may take advantage of the microclimate in the canopy and have less need for water with reduced transpiration forcing, whereas hydraulic constraints and nutrient limitations may become more important for taller trees in drier sites such as the low-elevation plot (cf. Martínez-Vilalta et al., 2009). Additionally, competition for limiting resources such as water or light will probably increase with canopy closure in drought-prone sites.

These findings also explain the greater climate sensitivity of dominant and large trees since the study sites are located in a drought-prone and nutrient-poor area (Montes et al., 2005; Gea-Izquierdo et al., 2015). The inverse relationship observed between spring–summer temperature and growth can be interpreted as an indirect influence of a water deficit on radial growth because warmer temperatures impair the soil–water balance through increased evapotranspiration (Abe and Nakai, 1999). The lagged response to previous summer-autumn precipitation might be related to more favorable conditions for carbohydrate synthesis and storage (Gimeno et al., 2012), growth of roots or enhanced bud develop-
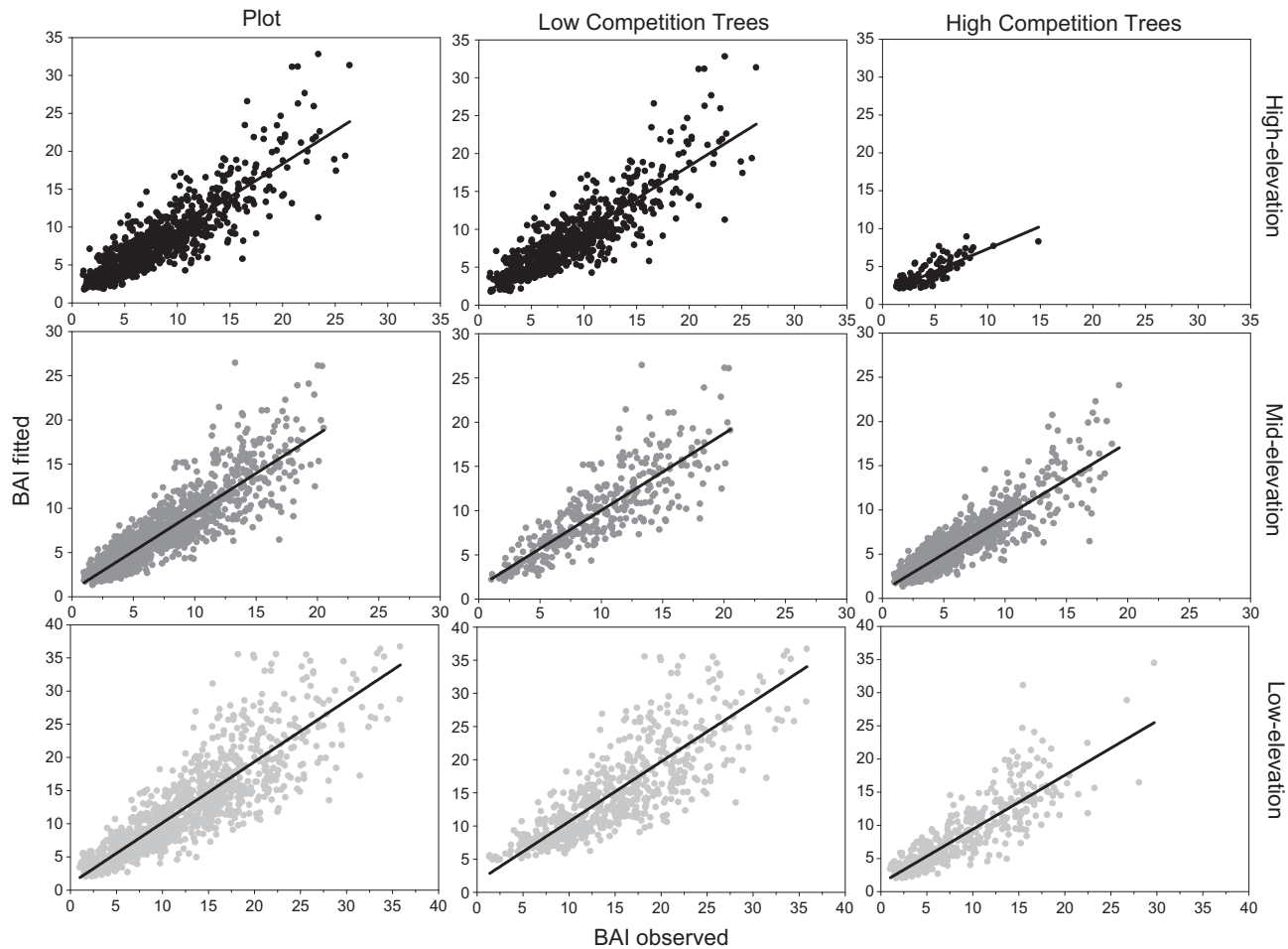
Fig. A5. Plot of fitted versus observed values of the basal area increment (BAI) for all the trees (plot, left column), and for low competition (LC) (middle column) and high competition (HC) trees (right column) in the high- (first row), mid- (second row) and low-elevation (third row) Scots pine plots.

ment (Pallardy, 2008). The size-dependent growth response to winter temperatures could be explained by an early snow melt and soil warming likely enhancing root growth of small shallow-rooted trees (Repo et al., 2008). On the other hand, mild winter temperatures would favor carbohydrate synthesis.

The significant effects of tree-level competition on the sensitivity of individual tree growth to climate reveal the importance of taking the stand structure into account when accurately designing management plans based on growth data in order to account for structural heterogeneity existing within any stand (Nehrbass-Ahles et al., 2014; Fernández-de-Uña et al., 2015). Past forest dynamics affect the adaptive capacity of trees to climate change as they modified the structure and determined present competition levels (Lindner et al., 2010). The variability in climate sensitivity among neighboring trees suggests proactive management practices are needed, to promote the adaptive capacity of forests. Thinning of formerly managed forests with recent regeneration could increase the range of size classes and reduce the vulnerability of forests to climate change (Millar et al., 2007; Giuggiola et al., 2013; Ruiz-Benito et al., 2014). Indeed, climate change has already influenced the growth of Iberian Scots pine forests during the past century (Andreu et al., 2007), for example, by reducing the thermal constraints at high-elevation sites (Sánchez-Salguero et al., 2015). Recent findings predict that high-elevation Mediterranean forests may also experience drought stress if warming continues (Galván et al., 2015). Therefore, managers should modify the stand structure by reducing competition for water in the most vulnerable tree populations, including high-elevation stands, to sustain the

provision of forest goods and services in the future when the climate will probably be warmer and drier (Huber et al., 2013). Finally, our results have implications for analyses based on static competition–growth relationships since we show that a dynamic approach is needed to adequately simulated forest dynamics, particularly in the context of rapidly changing climatic conditions.

Acknowledgments

Table A1
Linear mixed-effects models of the annual basal area increment (BAI) as a function of different climatic variables in the three Scots pine plots studied and located at different elevations (the selected model is marked in bold).

Plot	Model	k	AICc	Δi	Wi
High-elevation					
	P3 + P10 + Tx1	**5**	**751.38**	**0.00**	**81.18**
	P3 + P4 + Tx1	5	754.32	2.95	18.59
	P3 + P4 + P10 + Tx1	6	763.41	12.03	0.20
	Tx1	3	767.11	15.74	0.03
	P3 + P4 + P10 + Tx1 + Tx10	7	773.78	22.40	0.00
	P10	3	787.75	36.38	0.00
	Null model	2	826.28	74.91	0.00
Mid-elevation					
	P8 + P10 + Tx1 + Tx2 + Tx3	**7**	**1053.94**	**0.00**	**82.20**
	P8 + P10 + Tx1 + Tx2	6	1057.18	3.24	16.23
	P8 + P10 + Tx1 + Tx2 + Tx3 + Tx10	8	1062.92	8.98	0.92
	P8 + Tx1 + Tx2	5	1064.44	10.50	0.43
	P8 + P10 + Tx1 + Tx2 + Tx10	7	1065.78	11.84	0.22
	P4 + P8 + P10 + Tx1 + Tx2 + Tx3 + Tx7 + Tx10	10	1089.41	35.47	0.00
	Null model	2	1253.53	199.59	0.00
Low-elevation					
Low	**Tx1 + Tx2 + Tx9**	**5**	**1161.35**	**0.00**	**83.28**
	P5 + Tx1 + Tx2 + Tx3 + Tx9	7	1165.49	4.14	10.52
	P5 + Tx1 + Tx2 + Tx9	6	1167.07	5.72	4.76
	P5 + P8 + Tx1 + Tx2 + Tx3 + Tx9	8	1169.47	8.11	1.44
	P5 + P8 + P9 + Tx1 + Tx2 + Tx3 + Tx9	9	1186.44	25.09	0.00
	Tx1 + Tx9	4	1240.61	79.25	0.00
	Null model	2	1398.56	237.20	0.00

Abbreviations: k, number of parameters included in the model (number of explanatory variables plus the null model plus the error); AICc, Akaike information criterion corrected for small samples; Δi, difference in AICc with respect to the best-fitting model; Wi, Akaike weight, relative probability that the model i is the best-fitting model for the observed data. Climatic variables: Tx (maximum temperature) for 1-January, 2-February, 3-March, 7-July, 9-September, 10-October; P (precipitation) for 3-March, 4-April, 5-May, 8-August, 9-September and 10-October.

Table A2
Statistical parameters and partial variance explained by each model fitted to the basal area increment (BAI) of three Scots pine stands located at low-, mid- and high-elevation. The BAI models are based on: the competition index (CI), climatic variables (see Table 3) and the previous-year BAI (BAI$_p$). Parameters are presented for the selected final model including all trees, and separately for the low- (LC) and high-competition (HC) trees.

Models	Low-elevation		Mid-elevation		High-elevation	
	LC	HC	LC	HC	LC	HC
CI	10.18	27.76	7.31	27.53	13.98	35.58
Climate	50.58	34.73	64.36	30.52	55.96	19.00
BAI$_p$	16.50	12.86	5.75	10.25	4.96	7.98
Variance Explained (%)	77.26	75.35	77.42	78.30	74.90	62.57
Residuals error	32.74	24.65	22.58	21.70	25.10	37.43
No. trees	54	28	69	41	46	30

Appendix A

See Figs. A1–A5 and Tables A1 and A2.

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