

Title: Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change

Running title: neighborhood models and tree growth drivers

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1 Abstract

2 Most large-scale multi-species studies of tree growth have been conducted in tropical and
3 cool temperate forests, whereas Mediterranean water-limited ecosystems have received much
4 less attention. This limits our understanding of how growth of coexisting tree species varies
5 along environmental gradients in these forests, and the implications for species interactions
6 and community assembly under current and future climatic conditions. Here, we quantify the
7 absolute effect and relative importance of climate, tree size and competition as determinants
8 of tree growth patterns in Iberian forests, and explore inter-specific differences in the two
9 components of competitive ability (competitive response and effect) along climatic and size
10 gradients. Spatially-explicit neighborhood models were developed to predict tree growth for
11 the 15 most abundant Iberian tree species using permanent-plot data from the Spanish Second
12 and Third National Forest Inventory (IFN). Our neighborhood analyses showed a climatic
13 and size effect on tree growth, but also revealed that competition from neighbors has a
14 comparatively much larger impact on growth in Iberian forests. Moreover, the sensitivity to
15 competition (i.e. competitive response) of target trees varied markedly along climatic
16 gradients causing significant rank reversals in species performance, particularly under xeric
17 conditions. We also found compelling evidence for strong species-specific competitive
18 effects in these forests. Altogether, these results constitute critical new information which not
19 only furthers our understanding of important theoretical questions about the assembly of
20 Mediterranean forests, but will also be of help in developing new guidelines for adapting
21 forests in this climatic boundary to global change. If we consider the climatic gradients of this
22 study as a surrogate for future climatic conditions, then we should expect absolute growth
23 rates to decrease and sensitivity to competition to increase in most forests of the Iberian
24 Peninsula (in all but the northern Atlantic forests), making these management considerations
25 even more important in the future.

1 **Introduction**

2 Regeneration, growth and mortality are the main processes driving plant community
3 dynamics (Shugart 1984; Kohyama 1992; Oliver & Larson 1996). In plants, birth and death
4 are mediated by growth, since growth is usually negatively related to survival and positively
5 related to reproduction (Nakashizuka 2001; Wyckoff & Clark 2002; Pérez-Ramos *et al.*
6 2010). This renders understanding growth variation within and among populations a central
7 aspect of plant population and community ecology (Hara 1984; Stoll *et al.* 1994; Zavala *et al.*
8 2007; Coomes *et al.* 2009). Although the study of growth variation in multispecific forest
9 communities is not new, important advances have recently been made, as accessibility to
10 long-term forest inventories has facilitated the formulation of individual tree-based models at
11 large spatial scales and for many co-existing species (Uriarte *et al.* 2004; Canham *et al.* 2006;
12 Sánchez-Gómez *et al.* 2008; Purves 2009).

13 Most studies of growth variation have been conducted in tropical and cool temperate
14 forests, usually with the aim of understanding patterns and mechanisms of species
15 coexistence and biodiversity maintenance in the context of the neutral theory debate (e.g.
16 interspecific variation; Hubbell 2001; Uriarte *et al.* 2004; Coates *et al.* 2009), the mechanistic
17 plant competition theory (e.g. assembly trade-offs; Pacala *et al.* 1994; Lin *et al.* 2002) or the
18 metabolic theory (i.e. scaling of growth with other processes; Muller-Landau *et al.* 2006;
19 Russo *et al.* 2007). Mediterranean water-limited forests, however, have received much less
20 attention, resulting in a poor understanding of how different tree species respond along
21 environmental gradients in these forests and the implications for community assembly.
22 Moreover, understanding interspecific tree growth variation in Mediterranean ecosystems
23 may be crucial in a global change context, since these systems are among those most
24 threatened by global warming and land-use changes, and are therefore highly susceptible to

1 suffer dramatic changes in species range and abundance (Bakkenes *et al.* 2002; Schröter *et al.*
2 2005; Benito-Garzón *et al.* 2008).

3 As a result of climate change, temperature in the Mediterranean basin is expected to
4 increase while precipitation may decrease (Christensen *et al.* 2007). These changes could
5 have important direct effects on tree growth due to abiotic constraints (e.g. hydric stress) and
6 indirect effects due to increases in resource competition, as shown in a number of single-
7 species studies (Jump *et al.* 2006; Martín-Benito *et al.* 2008; Martínez-Vilalta *et al.* 2008;
8 Gea-Izquierdo *et al.* 2009; Linares *et al.* 2009; Vicente-Serrano *et al.* 2010). Multi-species
9 studies are, however, extremely rare, and tend to focus on a limited subset of species or a
10 given region (Sabaté *et al.* 2002; Andreu *et al.* 2007; Sánchez-Gómez *et al.* 2008). This
11 hampers our understanding of the likely effects of climate change not only on tree growth,
12 but also on plant-plant interactions, including competitive reciprocal effects and shifts in rank
13 hierarchies.

14 In recent decades, Mediterranean countries have also suffered large land use shifts
15 including agricultural land abandonment, reforestation of extensive areas with high tree
16 densities, and strict protection of many natural areas (Zavala & Oria 1995; Gómez-Aparicio
17 *et al.* 2009). All these practices have favored forest expansion and stand densification, and
18 have had a striking effect on tree growth patterns. For example, Linares *et al.* (2010) showed
19 that excessive protection of the endangered species *Abies pinsapo* in southern Spain increased
20 tree-to-tree competition and reduced the adaptive capacity of the species to drier climatic
21 conditions. All this suggests the need to explore competitive and tree growth responses along
22 tree density gradients, so that proper adaptation measures to cope with climatic changes can
23 be undertaken.

24 In this study, we used forest inventory data for continental Spain to analyze the effect
25 of climate, size and competition on tree growth of the 15 most abundant Iberian canopy

1 species using a spatially-explicit neighborhood scale approach. The main advantage of the
2 neighborhood approach is that it captures the local nature of plant interactions and
3 acknowledges that the frequency with which individuals interact with other conspecific or
4 heterospecific neighbors may depend less on their relative abundance than on their particular
5 spatial pattern (Silander & Pacala 1985; Wagner & Radosevich 1998; Stoll & Newbery 2005).
6 Specifically, we aimed to: 1) quantify the absolute effect and relative importance of climate,
7 size and competition on tree growth patterns in Iberian forests; 2) analyze how the sensitivity
8 to competition (i.e. *competitive response* or ability to withstand growth suppression by
9 neighbors, sensu Goldberg 1990) of the different species varied along climatic and size
10 gradients with potential consequences for the ranking of species performance; and 3) explore
11 whether different species of neighboring trees were functionally equivalent competitors (i.e.
12 have similar *competitive effects* or abilities to suppress neighbor growth, sensu Goldberg
13 1990) using inter-specific competition coefficients (i.e. the per capita effect of one species on
14 another, Freckleton & Watkinson 2001). By combining in the same analysis the three main
15 drivers of tree growth for the 15 most important tree species of the Iberian Peninsula, we
16 aimed to provide detailed quantitative information about how these factors interact to
17 determine growth of coexisting species at large spatial scales. This information will, in turn,
18 be crucial for predicting potential community-level consequences (e.g. rank reversals in
19 species performance) of growth alterations due to climate warming and human land use
20 change.

1 **Material and Methods**

2 *Data set*

3 Our analyses of tree growth were based on the Spanish Second and Third National Forest
4 Inventories (IFN2 and IFN3) conducted between 1986-1996 and 1997-2007, respectively
5 (Villaescusa & Díaz 1998; Villanueva 2004). The IFNs are extensive datasets consisting of
6 circular sample plots distributed across the forested surface of Spain, with an approximate
7 density of 1 plot Km⁻² across a large altitudinal gradient (sea level to 2330 m). Plots are of
8 various concentric radii (i.e. the minimum tree diameter measured varied with the radius of
9 the plot): all trees with diameter at breast height (d.b.h.) > 7.5 cm are measured within a 5-m
10 radius plot, trees with d.b.h. > 12.5 cm within a 10-m radius plot, trees with d.b.h. > 22.5 cm
11 within a 15-m radius plot, and trees with d.b.h. > 42.5 cm within a 25-m radius plot. We
12 limited our growth analyses to target trees within the smallest 5-m radius plot, considering as
13 neighbors those trees located within the 10-m radius plots. To compensate for the fact that
14 small trees (7.5 cm < d.b.h. < 12.5 cm) were measured only in the smallest 5-m radius plots,
15 we assumed that their density and size structure in these plots could be extrapolated to the
16 whole 10-m radius plot, and therefore generated “artificial” neighbor trees that were assigned
17 random positions within the outer 5 m of the 10-m radius plots. Thus, we obtained a full
18 census of all neighbors > 7.5 cm d.b.h. present at the beginning of the census interval (IFN2)
19 in a minimum radius of 5 m around each target tree. This radius size was consistent with that
20 used in other tree competition studies (Stoll *et al.* 1994; He & Duncan 2000; Boyden *et al.*
21 2005). Diameter growth of each target tree (in millimeters per year) between the two
22 censuses was calculated by dividing the total increase in d.b.h. (in millimeters) by the number
23 of years between the two census dates.

24 Each of the plots was characterized with 12 topographic and climatic variables. The
25 Iberian Peninsula is an area of transition between the Euro-Siberian, or temperate, and the

1 Saharo-Sindic climatic regions, and therefore contains a mosaic of different climates, from
2 humid Atlantic in the north to Mediterranean and semiarid in the center and south.
3 Topographic variables were calculated from a digital elevation model (COP 1998), and
4 climatic variables obtained through ordinary co-kriging from 5426 weather stations (series
5 1951-1999; Gonzalo 2008). Raster maps and plot locations (UTM coordinates) were
6 combined to determine the values of each abiotic variable in each plot using ArcView Gis 9.2
7 (ESRI Inc., Redlands, USA, 2000). The 12 abiotic variables were: *altitude*; *slope*; *annual* and
8 *seasonal* (i.e., *spring*, *summer*, *fall*, and *winter*) *precipitation*; *mean annual temperature*,
9 *mean temperature of the hottest month* and *mean temperature of the coldest month*; *drought*
10 *length*, taken as the number of months in which potential evapotranspiration exceeded
11 precipitation; and *drought intensity*, calculated on the basis of the quotient A_d/A_h , where A_d is
12 the dry area of the climodiagram (precipitation curve below the temperature curve) and A_h is
13 the humid area of the climodiagram (precipitation curve above the temperature curve, Allué-
14 Andrade 1990). The relationships between the 12 abiotic variables were explored with
15 Principal Component Analyses (PCA) based on correlations with varimax rotation. The first
16 axis of the PCA (explaining 36.1% of the variance) was strongly correlated ($r > 0.9$) with
17 mean annual temperature and mean temperature of the coldest month. The second axis
18 (explaining 36.0% of the variance) was strongly correlated with annual, spring and fall
19 precipitation. Therefore, for our modeling analyses we chose the two variables most
20 representative of each of the two axes: mean annual temperature and annual precipitation.

21

22 *A maximum-likelihood analysis of tree growth*

23 We used likelihood methods and model selection as an alternative to traditional hypothesis
24 testing for analysis of our data (Johnson & Omland 2004; Canham & Uriarte 2006).
25 Following the principles of likelihood estimation, we estimated model parameters that

1 maximized the likelihood of observing the growth data measured in the field given a suite of
2 alternative models.

3 We conducted separate analyses for the 15 most common canopy tree species. These
4 species present a wide range of functional traits, from deciduous temperate species typical of
5 northern cool Atlantic forests to evergreen Mediterranean oak and pine species from central
6 and southern Iberia (Table 1). We focused on abundant species (> 1000 individuals) because
7 small sample sizes can make it difficult to obtain competition coefficients for all neighbor
8 species (Coates *et al.* 2009). Our analyses of diameter growth of target trees estimated four
9 terms: 1) average potential diameter growth (PDG, in mm/year), and three sets of scalar
10 modifiers ranging from 0 to 1 that quantified the effects on average potential growth of 2)
11 local climatic conditions (expressed in terms of mean annual temperature and annual
12 precipitation), 3) initial target tree size (d.b.h., in cm), and 4) the characteristics of the
13 neighborhood. Our *full model* had the following form:

$$14 \quad \text{Growth} = \text{PDG} \times \text{Climatic effect} \times \text{Size effect} \times \text{Neighborhood effect} \quad (1)$$

15 *Potential diameter growth* (PDG) represents the expected target growth when the
16 other factors are at optimal values. The *climatic effect* was modeled using a bivariate
17 Gaussian function:

$$18 \quad \text{Climatic effect} = \exp \left[-\frac{1}{2} \left(\frac{T - X1_0}{X1_b} \right)^2 \right] * \exp \left[-\frac{1}{2} \left(\frac{P - X2_0}{X2_b} \right)^2 \right] \quad (2)$$

19 where $X1_0$ and $X2_0$ are the mean annual temperature (T) and annual precipitation (P) values,
20 respectively, at which maximum potential growth occurs; and $X1_b$ and $X2_b$ are estimated
21 parameters that control the breadth of the function (i.e. the variance of the normal
22 distribution). Equation 2 produces the classic Gaussian distribution of species performance
23 along an environmental axis usually assumed to describe vegetation-environment

1 relationships (e.g. Curtis 1959; Whittaker 1975; Gauch 1982), but can also produce sigmoidal,
 2 monotonic curves within restricted ranges of either axis. We also tested univariate functions
 3 in which terms for one of the two axes were dropped from the analysis.

4 Following recent studies (Uriarte *et al.* 2004; Canham *et al.* 2006; Coates *et al.* 2009),
 5 the *size effect* was modeled using a lognormal function:

$$6 \quad \text{Size effect} = \exp \left[-\frac{1}{2} \left(\frac{\ln(\text{dbh} / X3_0)}{X3_b} \right)^2 \right] \quad (3)$$

7 where $X3_0$ represents the target d.b.h. (cm) at which maximum growth occurs, and $X3_b$
 8 controls the breadth of the function. Depending on the value of $X3_0$, this functional form can
 9 be hump-shaped or monotonically increasing/decreasing.

10 The *neighborhood effect* was modeled as a function of a *neighborhood competition*
 11 *index* (NCI) using a Weibull function:

$$12 \quad \text{Neighborhood effect} = \exp \left[-a(\text{NCI})^b \right] \quad (4)$$

13 The Weibull function assumes that the neighborhood effect (and therefore target tree
 14 growth) declines monotonically as a function of NCI. A positive neighborhood effect was not
 15 considered in our models because an initial exploration of the data revealed that target growth
 16 always declined with increasing number or basal area of neighbors. The absence of a positive
 17 neighbor effect on target growth might be due to the fact that our analyses focused on adult
 18 trees and large saplings (d.b.h. > 7.5 cm), whereas facilitation decreases with ontogeny and it
 19 is mostly found for seedlings and small saplings (Miriti 2006; Quero *et al.* 2008). The NCI
 20 quantifies the net effect of $j=1, \dots, n$ neighboring trees of $i=1, \dots, s$ species on the growth of a
 21 target tree z . Following the long tradition of distance-dependence analysis of competition (e.g.
 22 Bella 1971; Daniels 1976), NCI was assumed to vary as a direct function of the size (d.b.h.)
 23 and an inverse function of the distance to neighbors following the form:

$$1 \quad \text{NCI} = \sum_{i=1}^s \sum_{j=1}^n \lambda_{iz} dbh_{ij}^{\alpha} \exp(-\gamma \text{distance}_{ij}^{\beta}) \quad (5)$$

2 where α , β and γ are parameters estimated by the analyses and determine the shape of the
 3 effect of the d.b.h. and the distance to the neighbor on NCI. In order to facilitate comparisons
 4 of neighborhood effects across target species, NCI values for each species were scaled
 5 relative to the maximum NCI found for that given species. This created a 0 to 1 index where
 6 0 and 1 represented the minimum and maximum neighborhood interactions observed for any
 7 target species.

8 We were particularly interested in exploring whether neighbor effects on a target
 9 species z varied between species or groups of neighbors. In order to do this, we multiplied the
 10 net effect of an individual neighbor by a per-capita competition coefficient (λ) that ranged
 11 from 0 to 1 and allowed for differences between species in their competitive effect on a target
 12 tree. Competition coefficients were only estimated for those species of competitors for which
 13 there were at least 100 neighbors. All remaining species of neighbors for that target species
 14 were then grouped into a "rare species" group. We tested four different groupings of
 15 neighboring species in Eqn. 5: 1) a model that calculated a different $\lambda_{i,z}$ value for each
 16 neighbor species, 2) a model that calculated two separate λ , one for conspecifics and another
 17 for heterospecifics, 3) a model that calculated two separate λ , one for conifers and one for
 18 angiosperms, and 4) a model in which all species were considered equivalent (i.e. fixing $\lambda =$
 19 1).

20 We also tested variants of Eqn. 4, in which sensitivity to competition varied as a
 21 function of climatic conditions (temperature and precipitation) and target tree size. For this,
 22 the exponential decay term (a) was allowed to vary as a function of mean annual temperature,
 23 annual rainfall and target d.b.h.:

$$24 \quad a = a' * \text{Temperature}^{\delta} * \text{Precipitation}^{\sigma} * dbh^{\theta} \quad (6)$$

1 If either δ , σ , or φ are = 0, then sensitivity to competition does not vary as a function of
2 temperature, precipitation or d.b.h. (respectively). If either δ , σ or φ are < 0, then sensitivity to
3 competition declines with temperature, precipitation or d.b.h. (i.e. at a given level of
4 competition, trees at lower temperatures and precipitation levels and with smaller d.b.h. will
5 suffer greater reductions in growth than trees at higher temperatures and precipitation levels
6 and with larger d.b.h.), and if either δ , σ , or φ are > 0 then sensitivity to competition increases
7 with climatic conditions and d.b.h.. These effects were assumed to be independent of the
8 underlying effect of climate or target tree size on potential growth (i.e. *climatic effect* or *size*
9 *effect*, in the absence of a *neighborhood effect*).

10

11 *Parameter estimation and model selection*

12 We used information theoretics (the Akaike Information Criterion, AIC) to select the best
13 growth model. Following the principle of parsimony, we employed the strategy of
14 systematically reducing the number of different parameters to the simplest model that was not
15 a significantly worse fit than any more complicated model. Thus, the full model was
16 compared to models that ignored the effect of climate, size, competition, or the three of them
17 (i.e. null, or intercept-only model), with lower AIC values indicating stronger empirical
18 support for a model (Burnham & Anderson 2002). Growth values were modeled using a
19 gamma error distribution defined by a shape parameter n , which varies from exponential-like
20 to bellshaped but left-skewed forms. We used simulated annealing, a global optimization
21 procedure, to determine the most likely parameters (i.e., the parameters that maximize the
22 log-likelihood) given our observed data (Goffe *et al.* 1994). The slope of the regression (with
23 a zero intercept) of observed radial growth on predicted radial growth was used to measure
24 bias (with an unbiased model having a slope of 1) and the R^2 of the regression was used as a
25 measure of goodness-of-fit. We used asymptotic two-unit support intervals to assess the

1 strength of evidence for individual maximum likelihood parameter estimates (Edwards 1992).
2 A support interval is defined as the range of the parameter value that results in less than a
3 two-unit difference in AIC. It is roughly equivalent to a 95% support limit defined using a
4 likelihood ratio test (Hilborn & Mangel 1997). All analyses were performed using software
5 written specifically for this study using Java (Java SE Runtime Environment v6, Sun
6 Microsystems Inc., California, USA, 2010).

1 **Results**

2 *Effects of climate, size and competition on potential tree growth*

3 A full model that included the effect on growth of all the factors explored (climate, size and
4 competition) was the best model for the 15 species analyzed (Table 2). However, the
5 competitive effect was always much stronger than the climatic or size effect, as indicated by
6 the larger increase in AIC when the competition term was dropped from the full models
7 (Table 2). All of the models produced unbiased estimates of growth (i.e. slopes of predicted
8 versus observed growth were all close to 1) and explained a percentage of variance in the data
9 (R^2) that ranged from 13% for *Quercus suber* to 34% for *Pinus nigra* (Table 2).

10 The effect of mean annual temperature on growth (Eqn. 2, see parameter values in
11 Appendix S1 of Supporting Information) varied widely among species, having a positive
12 effect on the 8 broadleaved species (particularly *F. sylvatica*), a negative effect on 5 conifers
13 (particularly *P. sylvestris*), and a neutral effect on 2 pine species (*P. pinea* and *P. uncinata*;
14 Fig. 1a). The effect of annual precipitation on growth (Eqn. 2, Appendix S1) was positive for
15 all species except *F. sylvatica*, presenting increased growth with precipitation either through
16 the entire precipitation range or reaching a peak at a lower precipitation level (Fig. 1b).

17 The 15 species showed 3 different patterns of variation in potential growth as a
18 function of target tree size (Eqn. 3, Appendix S1). Most pines showed a growth peak in the
19 15-25 cm size class range and a sharp decline in larger size classes (Fig. 1c). *Juniperus*
20 *thurifera* and broadleaved species reached a maximum growth peak at larger sizes than pines
21 (30-50 cm) and then showed moderate or slight declines in growth in larger size classes.
22 Finally, *Pinus pinea* was the only species for which size had virtually no effect on growth.

23 The magnitude of the negative effect of competition (calculated for a tree of mean size
24 under mean climatic conditions; Eqn. 4) was largest for conifers, with reductions close to
25 100% of potential growth under the maximum observed relative competition (i.e. NCI = 1;

1 Fig. 1d). Mediterranean evergreen broadleaves were the least sensitive to competition, with
2 reductions of 40-60% in potential growth at maximum competition levels. The α parameter
3 (Eqn. 5), which controls the effect of neighboring tree size on NCI, had values close to 2 for
4 conifers (range 1.76-1.96) and close to 1 for the rest of the species (range 0.76-1.40;
5 Appendix S1). These results indicate that competitive effects scale approximately linearly
6 with biomass (i.e. DBH^2) for conifers and with DBH for broadleaved species in Iberian
7 forests. The exponents β and γ (Eqn. 5) control the shape and the steepness (respectively) of
8 the effect of neighbor distance on NCI, and therefore on target tree growth. Conifers showed
9 faster declines in neighbor effects with distance than broadleaved species (Fig. 2).

10

11 *Variation in the competitive response of target species along climatic and size gradients*

12 Our analyses indicate that, for all species, sensitivity to competition varied markedly along
13 one or two of the climatic gradients explored (i.e. δ and/or $\sigma \neq 0$; Eqn. 6, Table 1). Atlantic
14 deciduous broadleaves had a lower competitive response ability at lower temperatures ($\delta < 0$;
15 Appendix S1), whereas the remaining species showed the opposite pattern ($\delta > 0$; Appendix
16 S1). For all species, trees at lower precipitation levels were more sensitive to competition
17 than trees located at wetter sites ($-0.22 < \sigma < -1.13$; Appendix S1). In all cases, smaller trees
18 were much more sensitive to competition than larger trees ($-0.35 < \phi < -1.50$; Appendix S1).

19 In order to explore the community-level consequences of the variation in sensitivity to
20 competition with climate and size, we analyzed shifts in growth hierarchies along the
21 competition gradient under two contrasting climatic scenarios, xeric ($T = 14^\circ\text{C}$, $PP = 600$ mm)
22 vs. mesic ($T = 8^\circ\text{C}$, $PP = 1500$ mm), and for two different size classes, small trees (d.b.h. = 10
23 cm) vs. large trees (d.b.h. = 40 cm). We found that larger shifts occurred in xeric rather than
24 in mesic habitats, and for small trees than for larger ones (Fig. 3). Thus, for 10-cm d.b.h. trees
25 in xeric habitats, conifers had the largest growth rates without competition, but were

1 displaced to the last positions of the ranking by broadleaved species at high competition
2 levels (Fig. 3a). Within each functional group (conifers vs. broadleaved), Mediterranean
3 species occupied the first positions of the ranking. On the other hand, basically no shifts
4 occurred for large trees in mesic habitats, with conifers (and particularly Mediterranean pines)
5 occupying the first places of the growth ranking along the whole competition gradient (Fig.
6 3d).

7

8 *Comparison of species competitive effects on tree growth*

9 For 11 of the 15 target tree species, the model that considered species-specific effects was the
10 most parsimonious of the four alternative models that differed in the grouping of neighbor
11 species (Table 2). For the remaining 4 species, the best model was the one that discriminated
12 between intra- and inter-specific competitors.

13 The competition indices (λ) estimated in the species-specific full models were used to
14 assemble a matrix of pairwise competition coefficients for the 15 tree species studied (Table
15 3). The magnitude of the competition coefficients was very large ($\lambda \geq 0.75$) in about 40% of
16 the cases, medium ($0.25 < \lambda < 0.75$) in 30% of the cases, and low ($\lambda \leq 0.25$) in the remaining
17 30%. Competition among conspecifics was generally strong (diagonal of λ with high values,
18 including maximum λ values [i.e. $\lambda = 1$] for more than half of the species). We explored the
19 existence of asymmetric pairwise interactions in the matrix (i.e. effect of species i on j [λ_{ij}]
20 much smaller/larger than the effect of species j on i [λ_{ji}]), but found no evidence for this
21 (Spearman rank correlation = -0.24, $p = 0.09$, $n = 48$).

1 **Discussion**

2 The use of nation-wide forest inventory data, spatially-explicit neighborhood models, and
3 information theoretics allowed us to quantify the effect of climate, tree size and competition
4 on the growth of the 15 most common tree species of the Iberian Peninsula. Our
5 neighborhood analyses revealed that, in Iberian forests, competition from neighbors is an
6 important driver of tree growth, causing much larger reductions in potential growth than
7 climate or tree size. Moreover, the sensitivity to competition (i.e. competitive response) of
8 target trees varied markedly along environmental gradients causing significant rank reversals
9 in species performance, particularly under xeric conditions. We also found compelling
10 evidence for strong species-specific competitive effects in these forests. Altogether, these
11 results constitute critical new information which not only furthers our understanding of the
12 assembly of Mediterranean forests, but will also be of help in developing new guidelines for
13 adapting forests in this climatic boundary to global change.

14

15 *Effects of climate and size on tree growth*

16 The response of growth to climate varied widely among species, particularly the response to
17 mean annual temperature. We found that rising temperatures generally had a positive effect
18 on growth of broadleaved species, particularly deciduous Atlantic species, but neutral or
19 negative effects on conifers, particularly on mountain pines (Fig. 1a). The positive effects of
20 temperature on broadleaved species' growth might arise from the fact that higher
21 temperatures may indicate longer growing seasons (Menzel & Fabian 1999; Peñuelas *et al.*
22 2002; Gordo & Sanz 2009). This would be especially true in cold sites such as those occupied
23 by Atlantic deciduous species, where the absence of frosts could favor early and late season
24 photosynthesis, increasing carbohydrate storage for future growth (Miyazawa & Kikuzawa
25 2005; Seynave *et al.* 2008; Vitasse *et al.* 2009). On the other hand, the negative effect of

1 increasing temperatures on conifer growth could be related to an increase in the atmospheric
2 water demand, causing greater drought stress at the sites occupied by these water-demanding
3 species (Barberó *et al.* 1998; Ferrio *et al.* 2003; Bogino & Bravo 2008). This indirect effect
4 of higher temperatures would be particularly apparent for pines typical of northern wetter
5 climates such as *P. sylvestris*, which persists at its southernmost distribution limit often at
6 high-altitude refuges (Castro *et al.* 2004).

7 The effect of precipitation on growth was much more uniform across tree species than
8 that of temperature. With the unexpected exception of *F. sylvatica*, all species showed higher
9 growth with increasing annual precipitation. This generalized positive effect of precipitation
10 is consistent with the limiting role that water plays in Mediterranean systems (e.g. Pigott &
11 Pigott, 1993), and with the recent evidence showing that Iberian tree species are becoming
12 increasingly water-stressed in summer (Andreu *et al.* 2007; Gea-Izquierdo *et al.* 2009).
13 Moreover, for several of the tree species analyzed here (e.g. *P. sylvestris*, *P. uncinata*, *F.*
14 *sylvatica*, *Q. robur*, *Q. petraea*) the Iberian Peninsula represents the edge of their southern
15 range, and thus they are already living at the limit of their physiological tolerances (Jump *et*
16 *al.* 2006; Reich & Oleksyn 2008; Martínez-Vilalta *et al.* 2010). An interesting prediction that
17 arises when putting together the species' responses to temperature and precipitation is that
18 alterations in temperature regimes due to climate change would be more likely to modify
19 inter-specific growth differences in forest communities than changes in precipitation. Thus,
20 whereas a reduction in precipitation could translate into a generalized decrease in growth, an
21 increase in temperature might cause a performance disadvantage of conifers compared to
22 broadleaves, particularly in northern Atlantic and montane sites where low temperatures are a
23 limiting factor for hardwoods expansion (Prentice *et al.* 1992; Terradas & Savé 1992;
24 Seynave *et al.* 2008).

25 The effect of target tree size on growth was quite variable among species. This result

1 agrees with previous studies for tropical and temperate forests, which have shown that the
2 size-growth relationship does not seem to follow a single rule (Muller-Landau *et al.* 2006;
3 Russo *et al.* 2007). The most common pattern found in Iberian tree species was a peak of
4 maximum growth at some intermediate DBH and subsequent decrease with size. This is also
5 probably the pattern of tree growth most frequently reported in other forest communities
6 (Ryan *et al.* 2004; Coates *et al.* 2009). However, this peak was generally reached at lower
7 sizes in conifers, which also showed a much steeper decrease with size than broadleaved
8 species (Fig. 1c). Therefore, despite the high variability found, we could conclude that the
9 magnitude of the size effect on growth in Iberian forests was larger for conifers than for
10 broadleaved species.

11

12 *Effect of competition on tree growth: variation in the competitive response of target species*
13 *along climatic and size gradients*

14 Although our results support a climate and size effect on tree growth in Iberian forests,
15 competition from neighbors had a comparatively much larger impact on growth for the 15
16 species analyzed (Fig. 1). Interesting differences emerged in the competitive response of the
17 studied species. Conifers in general, and mountain pines in particular, were the most sensitive
18 tree species to competition, with reductions close to 100% of potential growth under the
19 maximum observed relative competition. The high sensitivity of conifers to competition was
20 also reflected in the form of the competition kernel, which scaled faster with size (larger α
21 parameter) and decreased more steeply with distance (larger γ parameter; Fig. 2) than in
22 broadleaved species. At the other extreme, Mediterranean evergreen oaks were the most
23 resistant to competition, probably favored by their strategy of resource storage and
24 conservative use, which allows them to maintain very low growth rates (see low PDG values
25 in Appendix S1; Zavala *et al.* 2000; Ogaya *et al.* 2003). These results coincide with previous

1 studies conducted in Mediterranean forests which have suggested that pines are in general
2 less shade-tolerant than oaks and consequently more sensitive to competition from neighbors
3 (Zavala & Zea 2004; Sánchez-Gómez *et al.* 2006). In general, shade-intolerant species have
4 been found to require more "growing space" than shade-tolerant species (Burton 1993;
5 Simard & Sachs 2004).

6 Our results indicate that species' competitive responses are not constant, but vary
7 along climatic and size gradients. We found a more homogeneous interspecific response
8 along the precipitation gradient than along the temperature gradient. Thus, sensitivity to
9 competition increased with decreasing precipitation for all species, especially in the smallest
10 size classes. This result agrees with the idea that competition increases when resources are
11 more limiting (Tilman 1988), and specifically with the prediction that climate warming
12 would increase competition for water in Mediterranean forests (Cotillas *et al.* 2009; Linares
13 *et al.* 2010). Also, and in accordance with this prediction, sensitivity to competition increased
14 with increasing temperature for Mediterranean and sub-Mediterranean broadleaved species,
15 which could be linked to a higher transpirational demand and a decrease in water supply.
16 Atlantic deciduous broadleaved were once more the exception to the rule, their sensitivity to
17 competition increasing with decreasing temperature. This indicates that warmer temperatures
18 due to climate change could benefit these species not only by the direct climatic effect on
19 growth already discussed, but also indirectly by causing a release from competition.

20 A profound community-level consequence of the variation in sensitivity to
21 competition along climatic and size gradients was the occurrence of rank reversals in species
22 performance along the competition gradient under different environmental conditions. The
23 most abundant and clearest rank reversals occurred for early ontogenetic stages under xeric
24 conditions, with pines showing the highest growth under low competition intensity but the
25 lowest growth under high competition intensity (Fig. 3). In mesic environments, however, the

1 much higher absolute growth rates of pines than of broadleaved species compensated for their
2 higher sensitivity to competition, so they occupied the first places of the growth ranking at all
3 competition levels. Based on these results, an aridification of the Mediterranean climate due
4 to climate warming could cause rank reversals in multispecific forests, with conifers being at
5 a clear disadvantage due to their poorer ability to deal with resource shortages both above and
6 belowground in a warmer and more competitive environment.

7

8 *Inter-specific differences in competitive effects of neighbors on tree growth*

9 Our results offer strong support not only for a high variability of competitive responses
10 among coexisting tree species in Iberian forests, but also for species-specific competitive
11 effects of neighbors on target trees. Thus, on a per unit size basis, tree species cannot be
12 considered equivalent in Iberian forests, neither from a response nor an effect perspective.
13 The question of whether response and effect competitive abilities are linked in plant species
14 has received much attention due to its relevance for understanding the structure of plant
15 interactions (see Wang *et al.* 2010 and references therein). In this study, we did not find a
16 clear correlation between the competitive response and effect of tree species (Goldberg &
17 Landa 1991; Cahill *et al.* 2005; Fraser & Miletto 2008). For example, *P. halepensis* and *F.*
18 *sylvatica* had by far the largest competitive effects ($\lambda \sim 0.90$; Table 3), whereas they were not
19 characterized by particularly high or low competitive responses (Fig. 1d). The target-
20 neighbor interactions in these forests might therefore be the result of different combinations
21 of competitive abilities to tolerate and suppress neighbors.

22 We found that competitive interactions were in general of large magnitude,
23 particularly among conspecifics. To explore whether this result could be affected by the
24 spatial segregation of the species (i.e. that heterospecific neighbors were distinctively further
25 away from targets than conspecific neighbors) we examined the mean distance to both groups

1 of neighbors for the different species. Mean distances happened to be remarkably similar (data
2 not shown), so we did not find evidence for an influence of spatial segregation on the strong
3 negative neighbor effects on conspecifics. An alternative and more plausible explanation for
4 this result could lie in the resource partitioning hypothesis, which predicts more intense
5 competition among closely related individuals due to a higher similarity in the use of
6 resources (Tilman 1982; Argyres & Schmitt 1992; Uriarte *et al.* 2004). Previous studies have
7 also found density-dependent effects where nearby conspecifics decrease individual
8 performance to a much larger extent than heterospecifics (Stoll & Newbery, 2005; Zhao *et al.*
9 2006). It has been suggested that these types of negative density-dependent effects constitute
10 a mechanism for maintaining diversity in tropical forests (Janzen 1970; Wright 2002), and
11 they could also be acting in the much less diverse Mediterranean forests to promote species
12 coexistence at the neighborhood scale.

13

14 *Implications for management of Mediterranean forests under climate change*

15 Several of the key questions that scientists and managers currently face regarding the future
16 of Mediterranean forests concern their response to predicted climate change and the
17 mitigation tools available to increase their resilience to these changes. Our results clearly
18 indicate that although climate exerts considerable direct control over tree species
19 performance, its effect is modulated by biotic factors such as competition from neighbors.
20 Because competitive effects in these forests can suppress growth by almost 100%, species
21 can have a very limited capacity to respond to climate at high competition levels (Fig. 4).
22 Three main corollaries arise directly from these results. First, studies of climate change
23 effects on tree performance must necessarily consider stand structural characteristics,
24 something that has seldom been done so far (but see Hurteau *et al.* 2007; Gea-Izquierdo *et al.*
25 2009; Linares *et al.* 2009). Second, the reduction of competition by thinning should be

1 considered as an adaptation measure that could counteract the negative effects of climate
2 warming on tree performance (Cescatti & Piutti 1998; Gracia *et al.* 1999; Martín-Benito *et al.*
3 2010). Third, any management measure that promotes forest densification (e.g. abandonment
4 of thinning operations in reforestations, severe protection in natural areas) should be
5 evaluated carefully, since it could cause an increase in competition for resources (particularly
6 water) enhancing species vulnerability to a drier climate (Linares *et al.* 2010). If the climatic
7 gradients of this study can be considered as a surrogate for future climatic conditions, then we
8 should expect absolute growth rates to decrease and sensitivity to competition to increase in
9 most forests of the Iberian Peninsula (in all but the northern Atlantic forests), making these
10 management considerations even more important in the future.

11 Our neighborhood analyses also provide detailed recommendations to guide
12 silvicultural activities aimed at reducing competition. These activities should focus on
13 neighbors around small trees, which are by far the most sensitive to competition, and
14 prioritize the removal of close conspecifics in order to decrease negative density-dependent
15 effects. Neighborhoods of species (and particularly conifers) at their southern limit, such as *P.*
16 *sylvestris*, should also be a priority, since these species are the most sensitive to both climate
17 and competition. In summary, our results show that adapting forests to climate change can
18 greatly benefit from spatially-explicit information that indicates how competitive effects vary
19 with distance, size and identity of neighbors. Specifically, this knowledge will be essential to
20 evaluate which species mixtures, tree densities and size structures will perform better under a
21 given set of climatic conditions.

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Table 1. Sample sizes and mean [minimum - maximum] annual temperature (°C), annual rainfall (mm), target d.b.h. (cm) at the start of the growth period, number of neighbors in a 5-m radius plot, and basal area of neighbors (m²/ha) for the 15 study species.

Species	Acronym	Functional group	N° target trees	N° plots	Mean annual temperature	Annual rainfall	d.b.h.	N° Neighbors	Basal area
<i>Juniperus thurifera</i>	JUTH	Mediterranean conifer	2015	844	10.1 [8.1 - 14.6]	617 [366 - 1347]	13.2 [7.5 - 75.4]	3 [0 - 25]	0.71 [0 - 15.56]
<i>Pinus halepensis</i>	PIHA	Mediterranean conifer	15403	5139	13.8 [10.0 - 19.2]	517 [170 - 1484]	13.9 [7.5 - 70.]	4 [0 - 27]	0.99 [0 - 7.50]
<i>Pinus pinea</i>	PIPINE	Mediterranean conifer	3426	1435	14.9 [10.9 - 18.5]	642 [304 - 1682]	18.0 [7.5 - 96.1]	4 [0 - 46]	1.13 [0 - 9.48]
<i>Pinus pinaster</i>	PIPINA	Mediterranean conifer	16730	4867	12.2 [8.1 - 18.5]	742 [322 - 3058]	17.9 [7.5 - 71.6]	6 [0 - 46]	2.12 [0 - 14.57]
<i>Pinus nigra</i>	PINI	Mountain conifer	14409	3754	11.0 [6.3 - 18.3]	717 [360 - 2240]	13.4 [7.5 - 95.5]	7 [0 - 47]	1.70 [0 - 15.56]
<i>Pinus sylvestris</i>	PISY	Mountain conifer	22311	5063	9.2 [3.2 - 14.6]	920 [428 - 1977]	15.1 [7.5 - 128.3]	8 [0 - 45]	2.26 [0 - 17.96]
<i>Pinus uncinata</i>	PIUN	Mountain conifer	2286	546	6.0 [2.4 - 14.2]	1191 [667 - 1975]	16.0 [7.5 - 78.0]	7 [0 - 32]	2.55 [0 - 14.99]
<i>Quercus ilex</i>	QUIL	Mediterranean evergreen broadleaved	21700	7075	12.1 [6.6 - 18.6]	723 [268 - 1812]	10.5 [7.5 - 152.2]	7 [0 - 53]	1.13 [0 - 24.19]
<i>Quercus suber</i>	QUSU	Mediterranean evergreen broadleaved	3352	1360	15.1 [10.1 - 18.5]	799 [480 - 1862]	16.4 [7.5 - 106.6]	5 [0 - 30]	1.41 [0 - 15.42]
<i>Quercus pyrenaica</i>	QUPY	Sub-Mediterranean deciduous broadleaved	9004	2164	10.3 [5.9 - 16.4]	876 [460 - 2304]	11.1 [7.5 - 129.9]	9 [0 - 40]	1.56 [0 - 26.45]
<i>Quercus faginea</i>	QUFA	Sub-Mediterranean deciduous broadleaved	6123	2009	11.1 [5.8 - 18.3]	735 [409 - 1574]	10. [7.5 - 103.5]	8 [0 - 50]	1.41 [0 - 11.88]

Table 1. Extended

Species	Acronym	Functional group	N° target trees	N° plots	Mean annual temperature	Annual rainfall	d.b.h.	N° Neighbors	Basal area
<i>Quercus petraea</i>	QUPE	Atlantic deciduous broadleaved	1614	513	10.3 [4.0 - 16.2]	991 [540 - 2066]	12.4 [7.5 - 146.5]	8 [0 - 33]	1.70 [0 - 24.33]
<i>Quercus robur</i>	QURO	Atlantic deciduous broadleaved	1928	754	11.7 [6.4 - 14.7]	1273 [461 - 2236]	15.0 [7.5 - 127.3]	5 [0 - 30]	1.70 [0 - 17.82]
<i>Fagus sylvatica</i>	FASY	Atlantic deciduous broadleaved	4391	1032	9.0 [4.8 - 13.7]	1128 [587 - 2150]	14.4 [7.5 - 112.0]	8 [0 - 43]	2.40 [0 - 27.02]
<i>Castanea sativa</i>	CASA	Atlantic deciduous broadleaved	1138	436	12.3 [8.3 - 16.2]	1142 [637 - 2275]	14.3 [7.5 - 219.6]	7 [0 - 34]	1.84 [0 - 18.53]

Table 2. Comparison of the alternative models for the 15 target tree species using AIC. The four full models varied in their treatment of competition, considering species-specific competition, intra- vs. inter-specific competition, conifer vs. angiosperm competition, and equivalent competition. The “No climate”, “No size”, and “No comp.” models ignore the effect of climate, size, and competition, respectively. The best fitting model is given a Δ AIC value of zero (in bold), and the difference in AIC between this model and all others is reported.

Species	Δ AIC								δ	σ	ϕ	NP	Slope	R ²
	Full				No climate	No size	No comp.	Null						
	Species specific	Intra. vs inter.	Conif. vs Ang.	Equiv. comp.										
JUTH	5.2	0	12.8	1.9	7.4	8.9	137.1	149.9	Yes	Yes	Yes	15	1.01	0.14
PIHA	29.9	0	12.3	204.2	520.4	404.9	804.9	2481.6	Yes	Yes	Yes	13	1.00	0.26
PIPINE	0	23.8	33.9	50.8	52.3	2.2	410.5	580.8	Yes	Yes	Yes	19	0.99	0.25
PIPINA	0	82.0	49.6	85.2	335.1	4.9	1848.5	2805.7	Yes	Yes	Yes	25	1.00	0.29
PINI	0	66.2	78.1	155.2	197.7	65.2	2029.1	2959.2	Yes	Yes	Yes	30	0.99	0.34
PISY	0	245.4	287.3	254.5	159.3	115.4	2723.7	4034.4	Yes	Yes	Yes	30	1.00	0.30
PIUN	0	55.4	198.6	22.8	4.1	16.9	207.2	311.0	Yes	No	Yes	16	1.04	0.25
QUIL	0	40.0	396.4	44.3	2815.6	3021.6	2847.2	4056.4	Yes	Yes	Yes	30	0.99	0.14
QUSU	0	8.3	162.9	2.0	54.4	145.3	249.2	293.1	No	Yes	Yes	13	1.01	0.13
QUPY	8.2	0	4.7	2.5	208.1	382.9	889.9	1450.3	Yes	Yes	Yes	15	1.01	0.20
QUFA	0	20.5	76.7	75.1	185.5	299.1	489.1	1035.1	Yes	Yes	Yes	23	1.00	0.17
QUPE	0	16.9	39.5	40.6	32.3	100.7	106.6	264.9	Yes	No	Yes	20	1.01	0.21
QURO	0	19.8	7.4	23.6	41.7	46.6	105.5	204.7	Yes	No	Yes	19	1.00	0.16
FASY	3.3	0	147.6	193.2	221.9	225.3	363.3	1019.5	Yes	Yes	Yes	15	1.00	0.30
CASA	0	58.1	14.9	26.1	12.4	31.4	137.2	172.3	Yes	Yes	Yes	19	1.01	0.15

Notes: Species are identified with acronyms; see Table 1 for full names. The δ , σ and ϕ columns indicate whether (Y, yes; N, no) the best model included a term that allows sensitivity to competition to vary with mean annual temperature (δ), annual precipitation (σ) or target size (ϕ). NP is the total number of parameters in the best model. The slope and R² for the relationship between predicted and observed growth are also given.

Table 3. Per capita competition coefficients ($\lambda_{i,z}$) with 2-unit support intervals for the effects of a neighbor of species i on a target species z for the 15 most common tree species of the Iberian Peninsula.

On target ...	Effect of neighbor ...											
	JUTH	PIHA	PIPINE	PIPINA	PINI	PISY	PIUN	QUIL	QUSU	QUPY	QUFA	QUPE
JUTH	1 [0.75-1]	----	----	----	0.92 [0.85-1]	----	----	0.92 [0.60-1]	----	----	0.67 [0.43-0.87]	----
PIHA	----	1 [0.90-1]	0.13 [0-0.27]	0.01 [0-0.11]	0.04 [0-0.10]	0.84 [0.61-0.94]	----	0.04 [0-0.15]	0.01 [0-0.12]	----	0.22 [0-0.47]	----
PIPINE	----	1 [0.85-1]	0.67 [0.56-0.71]	0.17 [0-0.34]	----	----	----	0.49 [0.23-0.67]	0.02 [0-0.11]	----	----	----
PIPINA	----	1 [0.75-1]	0.69 [0.54-1]	0.40 [0.38-0.45]	0.48 [0.32-0.58]	0.36 [0.20-0.48]	----	0.31 [0.18-0.58]	0 [0-0.12]	0.01 [0-0.06]	0.70 [0.55-0.92]	----
PINI	0.95 [0.60-1]	0.94 [0.74-1]	----	0.47 [0.32-0.62]	1 [0.89-1]	0.86 [0.61-1]	----	0.85 [0.66-1]	----	0.01 [0-0.20]	0.00 [0-0.35]	0.06 [0-0.19]
PISY	0.80 [0.50-1]	0.38 [0.10-0.50]	----	0.31 [0.20-0.39]	1 [0.92-1]	0.63 [0.57-0.67]	0.25 [0-0.40]	0.65 [0.45-0.82]	----	0.00 [0-0.05]	0.39 [0.24-0.46]	0.01 [0-0.15]
PIUN	----	----	----	----	----	1 [0.91-1]	0.61 [0.55-0.68]	----	----	----	----	----
QUIL	0 [0-0.50]	0.98 [0.58-1]	0.34 [0.14-0.60]	0.02 [0-0.32]	1 [0.85-1]	1 [0.75-1]	----	0.75 [0.65-0.90]	0.06 [0-0.26]	0.23 [0.09-0.32]	0.31 [0.12-0.56]	0.95 [0.80-1]
QUSU	----	1 [0.70-1]	0.84 [0.55-1]	0.11 [0-0.37]	----	----	----	0.75 [0.60-0.90]	0.61 [0.51-0.76]	0.28 [0.11-0.33]	0.80 [0.62-0.95]	----
QUPY	----	----	----	0.87 [0.62-1]	0.71 [0.55-0.88]	0.92 [0.67-1]	----	1 [0.68-1]	0.80 [0.70-1]	1 [0.90-1]	1 [0.80-1]	0.98 [0.73-1]
QUFA	0.16 [0-0.30]	1 [0.95-1]	----	0.39 [0.12-0.61]	0.26 [0.11-0.32]	0.80 [0.55-1]	----	0.25 [0.05-0.39]	----	0.11 [0-0.23]	1 [0.95-1]	----
QUPE	----	----	----	----	0.52 [0.31-0.70]	0.96 [0.56-1]	----	0.23 [0-0.51]	----	0.29 [0-0.35]	----	1 [0.80-1]
QURO	----	----	----	0.26 [0-0.39]	----	----	----	0.96 [0.82-1]	----	0.33 [0.22-0.48]	----	----
FASY	----	----	----	----	----	0.06 [0-0.11]	----	0.02 [0-0.05]	----	0 [0-0.05]	0.76 [0.67-1]	0.01 [0-0.05]
CASA	----	----	----	0.01 [0-0.20]	----	----	----	0.55 [0.20-0.65]	----	1 [0.65-1]	----	----
Mean CE	0.58	0.91	0.53	0.27	0.66	0.74	0.43	0.56	0.25	0.30	0.59	0.50

Table 3. Extended

On target	Effect of neighbor ...		
	QURO	FASY	CASA
JUTH	----	----	----
PIHA	----	----	----
PIPINE	----	----	----
PIPINA	0 [0-0.13]	----	0 [0-0.36]
PINI	----	----	----
PISY	0.01 [0-0.09]	0.82 [0.60-1]	----
PIUN	----	----	----
QUIL	0.05 [0-0.19]	1 [0.80-1]	0.83 [0.72-1]
QUSU	----	----	----
QUPY	0.73 [0.58-1]	0.91 [0.76-1]	0.71 [0.60-1]
QUFA	----	0.94 [0.79-1]	----
QUPE	----	0.65 [0.40-0.90]	----
QURO	1 [0.85-1]	----	0.03 [0-0.25]
FASY	0.53 [0.37-0.72]	1 [0.94-1]	----
CASA	0.84 [0.54-1]	----	0.53 [0.39-0.69]
Mean CE	0.35	0.90	0.44

Notes: Species are identified with acronyms; see Table 1 for full names. Coefficients were estimated only when there were at least 100 neighbors of that species (dashed lines otherwise). The competition coefficients are scaled so that the strongest competitor for each target tree species has a value of 1. Conspecific

interactions are shown in bold. Also shown is the mean competitive effect (CE) of each neighbor species on all target species for which it was a common neighbor.

Figure legends

Figure 1. Predicted effect of a) mean annual temperature, b) annual precipitation, c) target tree size, and d) NCI (neighborhood competition index) on growth for the 15 most common tree species of the Iberian Peninsula. The effects of climate and size are calculated in the absence of competition. The effect of competition is calculated for a tree of mean size at mean climatic conditions (see Table 1 for mean values). See Appendix 1 for the estimated parameters of the corresponding functions. See Table 1 for key to species abbreviations.

Figure 2. Predicted variation of NCI (neighborhood competition index) with distance to neighbors for the 15 target tree species studied. To simplify presentation of results, the parameter α was set to zero in Eqn. 5. See Table 1 for key to species abbreviations.

Figure 3. Predicted variation in potential growth along a competition gradient for four different combinations of climatic and tree size conditions: a) small trees (d.b.h. = 10 cm) in xeric sites ($T = 14^{\circ}\text{C}$, $P = 600$ mm); b) large trees (d.b.h. = 40 cm) in xeric sites; c) small trees (d.b.h. = 10 cm) in mesic sites ($T = 8^{\circ}\text{C}$, $P = 1500$ mm); and d) large trees (d.b.h. = 40 cm) in mesic sites. See Appendix 1 for the estimated parameters of the corresponding functions. See Table 1 for key to species abbreviations.

Figure 4. Predicted variation in potential growth of *Pinus sylvestris* along a temperature and competition gradient for two size classes: a) d.b.h. = 10 cm, and b) d.b.h. = 40 cm. Observe how the response to temperature is almost null at high competition levels (i.e. $\text{NCI} = 1$), particularly for small trees.

Appendix S1. Parameter estimates and 2-unit support intervals (in brackets) for the best model selected for each of the 15 target tree species. See text for a description of the parameters.

Species	PDG	X1 ₀	X1 _b	X2 ₀	X2 _b	X3 ₀	X3 _b
<i>Juniperus thurifera</i>	4.44 [4.39-4.49]	2.35 [2.34-2.36]	18.98 [18.97-18.99]	1994.38 [1994.37-1994.39]	1537.90 [1537.88-1537.92]	49.47 [49.46-49.48]	2.95 [2.90-3.00]
<i>Pinus halepensis</i>	8.72 [8.62-8.82]	1.65 [1.64-1.66]	30.13 [30.12-30.14]	1002.05 [1002.03-1002.06]	729.77 [727.87-730.97]	24.88 [24.33-25.68]	1.33 [1.28-1.38]
<i>Pinus pinaster</i>	12.40 [12.39-12.41]	2.60 [2.59-2.61]	18.20 [18.19-18.21]	1884.71 [1884.70-1884.72]	1577.19 [1577.18-1577.20]	23.30 [23.29-23.31]	1.45 [1.44-1.46]
<i>Pinus pinea</i>	8.25 [8.20-8.30]	20.61 [20.60-20.62]	260.32 [260.31-260.33]	1100.45 [1100.44-1100.46]	760.64 [760.63-760.65]	26.68 [26.63-26.73]	5.63 [5.58-5.68]
<i>Pinus nigra</i>	9.39 [9.35-9.43]	0.47 [0.42-0.52]	11.59 [11.54-11.64]	2569.75 [2569.70-2569.80]	2131.21 [2131.16-2131.26]	18.68 [18.64-18.74]	1.05 [1.00-1.10]
<i>Pinus sylvestris</i>	9.13 [9.12-9.14]	1.09 [1.08-1.10]	11.75 [11.74-11.76]	2386.82 [2386.81-2386.83]	2660.83 [2660.82-2660.84]	19.92 [19.91-19.93]	1.11 [1.10-1.12]
<i>Pinus uncinata</i>	6.52 [6.47-6.65]	71.59 [71.58-71.60]	230.38 [230.37-230.39]	1369.72 [1369.71-1369.73]	2999.98 [2999.97-2999.99]	15.57 [13.86-17.17]	1.44 [1.29-1.96]
<i>Quercus ilex</i>	3.96 [3.91-4.01]	25.81 [25.80-25.82]	24.52 [24.51-24.53]	1262.49 [1262.48-1262.50]	1031.06 [1031.05-1031.07]	25.97 [25.92-26.02]	1.75 [1.70-1.80]
<i>Quercus suber</i>	4.15 [4.14-4.16]	28.56 [28.55-28.57]	38.79 [38.78-38.80]	1614.59 [1614.58-1614.60]	1963.27 [1963.26-1963.28]	81.81 [81.79-81.82]	2.81 [2.80-2.82]
<i>Quercus pyrenaica</i>	5.24 [5.19-5.36]	18.10 [18.09-18.11]	12.16 [12.15-12.17]	1172.17 [1172.16-1172.18]	1642.55 [1642.54-1642.56]	43.07 [43.02-43.12]	1.68 [1.63-1.73]
<i>Quercus faginea</i>	5.27 [5.22-5.32]	37.21 [37.20-37.22]	26.16 [26.15-26.17]	1297.80 [1297.79-1297.81]	1147.10 [1147.09-1147.11]	52.99 [52.94-53.04]	1.70 [1.65-1.75]
<i>Quercus petraea</i>	5.01 [4.95-5.05]	25.41 [25.40-25.42]	21.80 [21.79-21.81]	1021.65 [1021.64-1021.66]	2820.18 [2820.17-2820.19]	34.15 [34.10-34.20]	1.33 [1.28-1.38]
<i>Quercus robur</i>	9.60 [9.55-9.65]	27.76 [27.75-27.77]	14.68 [14.67-14.69]	1316.30 [1316.29-1316.31]	977.04 [977.03-977.05]	47.54 [47.49-47.59]	1.84 [1.79-1.89]
<i>Fagus sylvatica</i>	7.52 [7.47-7.57]	19.79 [19.78-19.80]	10.10 [10.09-10.11]	254.71 [254.70-254.72]	1670.40 [1670.39-1670.41]	43.41 [43.36-43.46]	1.38 [1.33-1.43]
<i>Castanea sativa</i>	8.15 [8.10-8.20]	22.52 [22.51-22.53]	15.55 [15.54-15.56]	1303.24 [1303.23-1303.25]	1263.07 [1263.06-1263.08]	26.75 [26.70-26.80]	1.67 [1.62-1.72]

Appendix S1. Extended

Species	a	b	α	β	γ	δ	σ	φ	n
<i>Juniperus thurifera</i>	195.23 [195.20-195.26]	1.00 [1-1.05]	1.76 [1.72-1.82]	1.13 [1.11-1.14]	0.18 [0.17-0.19]	0.10 [0.09-0.11]	-0.56 [-0.57 to -0.55]	-0.53 [-0.54 to -0.52]	1.58 [1.53-1.63]
<i>Pinus halepensis</i>	144.26 [144.25-144.27]	1.00 [1-1.05]	1.80 [1.75-1.85]	0.80 [0.74-0.87]	0.43 [0.39-0.49]	0.39 [0.38-0.40]	-0.23 [-0.24 to -0.22]	-1.53 [-1.54 to -1.52]	2.24 [2.19-2.29]
<i>Pinus pinaster</i>	282.43 [282.31-282.56]	1.00 [1-1.01]	1.96 [1.94-2.00]	0.50 [0.47-0.54]	0.63 [0.56-0.71]	0.54 [0.53-0.55]	-0.41 [-0.42 to -0.40]	-1.19 [-1.20 to -1.18]	2.19 [2.14-2.20]
<i>Pinus pinea</i>	25.88 [24.78-26.66]	1.00 [1-1.05]	1.82 [1.77-1.86]	0.91 [0.79-1.16]	0.13 [0.08-0.25]	0.19 [0.18-0.20]	-0.84 [-0.85 to -0.83]	-0.57 [-0.58 to -0.56]	2.25 [2.24-2.26]
<i>Pinus nigra</i>	186.39 [184.42-188.01]	1.00 [1-1.05]	1.92 [1.90-1.94]	0.75 [0.74-0.76]	0.58 [0.56-0.61]	0.11 [0.10-0.12]	-0.19 [-0.20 to -0.18]	-1.23 [-1.24 to -1.22]	1.97 [1.92-2.02]
<i>Pinus sylvestris</i>	78.56 [78.55-78.57]	1.00 [1-1.01]	1.79 [1.76-1.80]	0.61 [0.60-0.62]	0.81 [0.79-0.83]	0.32 [0.31-0.33]	-0.13 [-0.14 to -0.12]	-1.11 [-1.12 to -1.10]	2.24 [2.22-2.26]
<i>Pinus uncinata</i>	22.49 [22.48-22.50]	1.00 [1-1.05]	1.80 [1.76-1.86]	1.13 [1.09-1.17]	0.32 [0.29-0.35]	0.27 [0.26-0.28]		-1.05 [-1.03 to -1.06]	1.79 [1.78-1.80]
<i>Quercus ilex</i>	0.52 [0.49-0.61]	1.00 [1-1.01]	0.98 [0.89-1.08]	7.47 [7.01-8.03]	0.00 [0-0.20]	0.71 [0.70-0.72]	-0.05 [-0.06 to -0.04]	-0.39 [-0.40 to -0.38]	1.65 [1.64-1.66]
<i>Quercus suber</i>	412.75 [412.64-412.82]	1.00 [1-1.01]	0.95 [0.81-1.23]	6.59 [6.10-6.74]	0.00 [0-0.38]		-0.73 [-0.75 to -0.70]	-0.58 [-0.59 to -0.56]	1.53 [1.52-1.54]
<i>Quercus pyrenaica</i>	134.00 [133.99-134.01]	1.00 [1-1.05]	1.36 [1.35-1.38]	4.64 [3.98-4.92]	0.00 [0-0.15]	0.11 [0.10-0.12]	-0.12 [-0.13 to -0.11]	-1.57 [-1.56 to -1.58]	2.02 [1.97-2.07]
<i>Quercus faginea</i>	717.19 [717.18-717.20]	1.00 [1-1.05]	1.25 [1.10-1.44]	6.92 [5.28-7.56]	0.00 [0-0.05]	-0.50 [-0.54 to -0.44]	-0.26 [-0.30 to -0.20]	-1.41 [-1.42 to -1.40]	2.29 [2.24-2.34]
<i>Quercus petraea</i>	41.53 [41.51-41.54]	1.00 [1-1.05]	1.38 [1.34-1.42]	3.60 [3.12-3.99]	0.00 [0-0.35]	-0.25 [-0.26 to -0.24]		-1.13 [-1.14 to -1.12]	1.92 [1.87-1.97]
<i>Quercus robur</i>	82.77 [82.76-82.78]	1.01 [1-1.05]	1.40 [1.39-1.50]	0.90 [0.81-1.02]	0.20 [0.18-0.23]	-0.95 [-0.98 to -0.91]		-0.59 [-0.63 to -0.54]	1.57 [1.47-1.61]
<i>Fagus sylvatica</i>	1820.59 [1820.58-1820.60]	1.00 [1-1.05]	1.31 [1.28-1.36]	0.83 [0.69-1.03]	0.24 [0.19-0.36]	-0.90 [-0.91 to -0.89]	-0.29 [-0.30 to -0.28]	-1.07 [-1.08 to -1.05]	1.39 [1.34-1.44]
<i>Castanea sativa</i>	392.61 [392.60-392.62]	1.00 [1-1.05]	0.76 [0.61-1.16]	4.56 [3.87-5.03]	0.00 [0-0.05]	-0.32 [-0.33 to -0.31]	-0.33 [-0.34 to -0.32]	-0.95 [-0.98 to -0.92]	1.98 [1.97-1.99]