Rank reversals in tree growth along tree size, competition and climatic gradients for four forest canopy dominant species in Central Spain*

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Abstract –
• Interspecific differences in tree growth patterns with respect to biotic and abiotic factors are key for understanding forest structure and dynamics, and predicting potential changes under climate change.
• Repeated observations from the Spanish Forest Inventory (SFI) were used to parameterize maximum likelihood estimators of tree growth as a function of tree size, competition indices and climate for *Pinus pinaster*, *P. sylvestris*, *Quercus ilex* and *Q. pyrenaica*.
• Significant responses to both biotic and abiotic factors were found, with interspecific differences in species performance along competition, temperature and precipitation gradients. *Q. ilex* was the species most tolerant to competition while *P. pinaster* was the species most sensitive to climatic variation. Species relative positions shifted along gradients of these factors with rank reversals in species performance along size, competition and climatic gradients.
• The results based on average growth matched previous forestry classifications and experimental studies on relative growth rate (RGR).
• When examining growth along studied abiotic and biotic gradients, a mismatch was found between species performance ranks as predicted by our models and information derived from previous knowledge. Those discrepancies highlight the relevance of ontogeny and environmental heterogeneity in defining species performance along competition gradients.

niche differentiation / *Pinus pinaster* / *Pinus sylvestris* / *Quercus ilex* / *Quercus pyrenaica*

Résumé – Interversion de rangs dans la croissance des arbres en relation avec la taille de l'arbre, la compétition et les gradients climatiques pour quatre espèces forestières dominantes dans la canopée.
• Les différences interspécifiques dans les modèles de croissance des arbres, pour ce qui concerne les facteurs biotiques et abiotiques, sont des clés pour la compréhension des structures et des dynamiques forestières, et pour prédire les changement potentiels avec le changement climatique.
• Des observations répétées de l'Inventaire Forestier Espagnol (SFI) ont été utilisées pour paramétrer les estimateurs de probabilité maximum de croissance des arbres comme une fonction de la taille de l'arbre, des indices de compétition et du climat pour *Pinus pinaster*, *Pinus sylvestris*, *Quercus ilex* et *Quercus pyrenaica*.
• Des réponses significatives aux facteurs biotiques et abiotiques ont été trouvées, avec des différences interspécifiques pour les performances des espèces en relation avec la compétition, les gradients de température et de précipitations. *Quercus ilex* a été l'espèce la plus tolérante à la compétition tandis que *Pinus pinaster* a été l'espèce la plus sensible aux variations climatiques. Les positions relatives des espèces ont changé en relation avec les gradients de ces facteurs avec des interversions de rang pour les performances des espèces en relation avec la taille, la compétition et les gradients climatiques.
• Les résultats basés sur la moyenne de croissance sont en adéquation avec la classification forestière antérieure et les études expérimentales sur le taux relatif de croissance (RGR).
• En examinant la croissance en relations avec les gradients biotiques et abiotiques étudiés, il a été trouvé une disparité entre les rangs de performance des espèces prédits par nos modèles et les informations provenant des connaissances antérieures. Ces divergences soulignent l'importance de l'ontogénie et de l'hétérogénéité environnementale pour la détermination des performances des espèces en relation avec les gradients de compétition.

niche de différenciation / *Pinus pinaster* / *Pinus sylvestris* / *Quercus ilex* / *Quercus pyrenaica*

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1. INTRODUCTION

Interspecific differences in tree growth are considered among the key factors driving forest succession, along with

other processes such as mortality and seedling recruitment (Huston and Smith, 1987; Shugart, 1984). Tree growth is determined by the availability of resources, the current state of the tree and the tree's genetic background. Important resources influencing growth are light, water, CO_2, nutrient availability and temperature (Lambers et al., 1998). Climate influences the spatial and temporal availability of these resources, particularly through direct effects on water availability and temperature (e.g. Lough, 1997; Varis et al., 2004). Competition between trees affects resource availability (Tilman, 1982), and therefore tree growth. Tree growth varies also with age and size since increasing size affects the ability of an individual to acquire resources (Wyckoff and Clark, 2005).

Despite the extensive literature on dendroecology (e.g. Andreu et al., 2007; Cherubini et al., 2003) and physiological mechanisms linked to tree growth (e.g. Montgomery, 2004; Pereira, 1994) the causes and community-level consequences of interspecific variation in tree growth remain poorly understood, even for many canopy dominant species. Chiefly, interspecific differences found on physiological- or morphological-level may not translate into divergence in whole-plant performance (Givnish, 1988). Moreover individual species variation can change along climatic and competition gradients (Begon et al., 1996; Whittaker, 1975), and ontogeny (Coleman et al., 1994), resulting in rank reversals in species performance along environmental gradients (Baraloto et al., 2005; Chesson, 1985). Those rank reversals are the key for understanding and identifying potential trade-offs which establish the functional basis for niche differentiation and species coexistence (Kitajima and Poorter, 2008). In other words, rank reversals in species performance along environmental gradients provide important clues to understand forest structure and dynamics along environmental gradients.

Traditionally, lack of individual species performance data has hampered the development and application of mechanistic theories of forest dynamics which often rely on intensive and detailed field data costly to obtain (Pacala et al., 1996). Recent availability of extensive data sets on tree distribution and performance along with numerically intensive statistical tools for model parameterization offer currently new avenues for multi-species comparison.

In this study, we analyzed data from the Spanish Forest Inventory (hereafter SFI) (DGCN, 2004; ICONA, 1994) to parameterize models of tree growth as a function of tree size, climatic variation and tree competition in central Spain. In the current context this approach is preferred over whole stand models because it allows describing the behavior of the stand or the community in terms of individual tree performance which is useful both from a theoretical (e.g. Levin, 1992; Zavala et al., 2007) and an applied perspective (Pukkala and Kolström, 1988).

In our study area, a sharp climatic gradient (reflected in the transition from Mediterranean to mesic or montane forests) occurs within approximately 50 km. The overstory of these forests is dominated by four species, *Quercus ilex* L. spp. *ballota* (holm-oak), *Q. pyrenaica* Willd. (sessile oak), *P. pinaster* Ait. (maritime pine), *Pinus sylvestris* L. (Scots
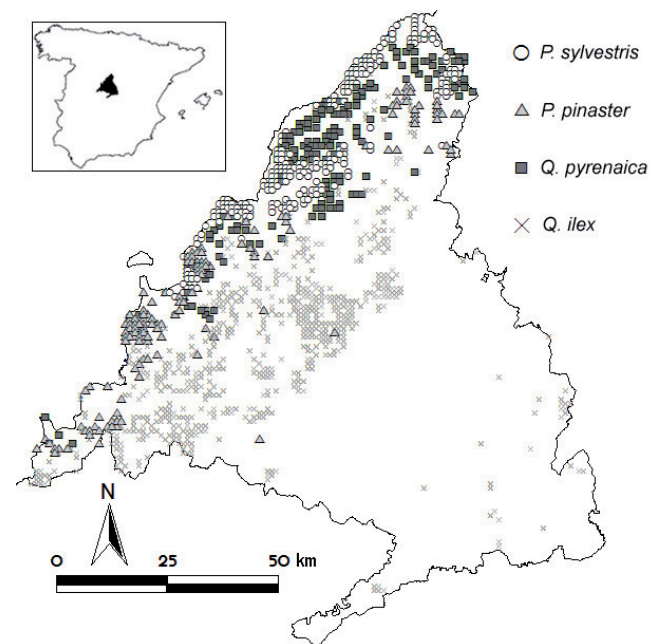

Figure 1. Map of the study region (province of Madrid, central Spain) including the distribution of the target species based on the SFI plots.

pine), which are representative of Mediterranean and montane forests throughout the Iberian Peninsula (Costa et al., 1998).

First, we tested a number of functional responses and independent variables to investigate the main factors (chiefly initial size, competition intensity and the climatic factors temperature and precipitation) influencing tree growth. Second, we tested for the existence of interspecific differences in tree growth along these biotic and abiotic factors and examine the agreement with previous qualitative forestry classifications and experimental data. Finally, we tested for the existence of rank reversals in tree growth along these factors.

2. MATERIALS AND METHODS

2.1. Study region and species

The study site comprises Madrid autonomous region located in the centre of the Iberian Peninsula (Fig. 1). It covers a surface area of 8 028 km², approximately 1.6% of Spain's total territory. This region spans 39° 53' N to 41° 10' N and 3° 03' W to 4° 34' W, encompassing an altitudinal gradient that ranges from 470–2400 m. The climate is quite variable with mean annual precipitation ranging from 300 mm to 1900 mm, warm summers (average July temperature: 14 to 24 °C) and fairly cold winters (average January temperature: –1 to 6 °C). The landscape is a mosaic of semi natural forests, savannas, shrublands, grasslands, intensive agricultural fields and urban areas (Purves et al., 2007).

The target species dominate the forest overstory throughout the Iberian Peninsula and are found in more than 85% of the forest stands in this region (DGCN, 2004). *P. pinaster*, *Q. ilex* and *Q. pyrenaica* have a typical Mediterranean distribution while *P. sylvestris*

has a wider distribution along the Eurosiberian region also including the Mediterranean Basin (Costa et al., 1998). *Q. ilex* is a sclerophyllous Mediterranean oak more drought tolerant than *Q. pyrenaica* which has been classified as a nemoro-Mediterranean oak (Corcuera et al., 2002). *P. pinaster* is considered more drought tolerant than *P. sylvestris*. The former grows in montane areas with irregular precipitation and high temperatures in summer, while the latter is frequently found at a higher altitude mainly in northern aspects, with higher precipitation and mild temperatures (Bravo-Oviedo et al., 2006). The spatial distribution of these species in the study region is represented in Figure 1.

2.2. Data collection and processing

The SFI consists of a systematic sampling of permanent plots distributed on a square grid of 1 km onto forest areas, with a remeasurement interval of 10-years approximately. Plots were circular, of four concentric radii. Inclusion of a tree in the sample was function of its diameter at breast height (dbh, 1.3 m), and its distance from the centre of the plot: 5 m radius was used for trees with dbh between 7.5–12.49 cm; 10 m for 12.5–22.49 cm; 15 m for 22.5–42.49 cm; and 25 m for dbh $\geq$ 42.5 cm. For the purpose of this study data have been obtained from the second (2-SFI) and third (3-SFI) inventories carried out in Madrid in the period 1994 to 2004. We first combined and filtered all data from 2-SFI and 3-SFI discarding those errors of negative diameter or height growth, or with changes in species identity. We extracted a number of variables from the combined database including two perpendicular values for dbh (mm), tree height (m) and UTM coordinates. Climatic data such as annual mean temperature (°C) and annual mean precipitation (mm) were provided by the Spanish Institute of Meteorology, as an interpolation of the information recorded in meteorological stations from 1971 to 2000 with 1 km spatial resolution (INM unpublished). Individual tree basal area was calculated as:

$$B = \frac{\pi}{4} \cdot d_1 \cdot d_2 \qquad (1)$$

where *B* stands for basal area (cm^2) and 'd_1, d_2' for the two perpendicular stem diameters (cm) at breast height. Because of the particular sampling method of the SFI based on variable-radius concentric plots, the basal area was scaled up to a one-hectare area. Basal area growth was calculated as:

$$\Delta B = B_{SFI-3} - B_{SFI-2} \qquad (2)$$

where B_{SFI-3} and B_{SFI-2} stand for basal area in the third SFI and the second SFI respectively.

We only selected those inventory plots where one of the four studied species, contributed at least to 95% of the total basal area of the plot. Such 'monospecific' stands for these species represent more than 86% of all the inventory plots in this region (i.e., 1180 plots) accounting for a total of 8010 individuals (1870 individuals for *Q. ilex*, 1,069 for *Q. pyrenaica*, 3,556 for *P. sylvestris* and 1515 for *P. pinaster*).

A number of distance-independent competition indices were also calculated that estimated the competition intensity on the subject tree as the total density or basal area of neighbouring trees per hectare. Half of these indices were one-sided competition indices that took into account only taller trees than the subject tree, while two-sided competition indices considered all neighbours and excluded the subject tree for calculations (see a full description of competition indices in Tab. I).

2.3. Model formulation and comparison

We modeled individual basal area growth for each of the four studied species. A gamma error distribution of basal area was assumed as it captured the whole range of variation observed in tree growth distributions. This distribution is defined by a scale parameter *a* and a shape parameter *n* that measures left-skewness. We specified the mean of the gamma distribution ($a \times n$) as a function of initial size (S, as the basal area in 2-SFI), competition (C, as the value of a competition index), mean annual temperature (T) and mean annual precipitation (P). Other climatic predictors such as aridity indices (Dantin and Revenga, 1940; De Martonne, 1926) were first considered but they systematically rendered poorer fits to the growth models and were therefore not included in the final model. We tested different functional forms that covered a wide range of possible responses: linear, Michaelis Menten-type, power, exponential and hyperbolic. They were separately tested for each competition index. The models presented here (Tab. II) are just a representative sample of the various combinations that were evaluated. Specifically, we report models that resulted in the best fit within each functional form tested. Since the scale resolution of the models is defined by the plot (1 km^2), independence of trees within the same plot is assumed.

Models were parameterized using a simulating annealing algorithm (Metropolis et al., 1953), and compared by likelihood (Edwards, 1992) and differences in Akaike's Information Criteria (ΔAIC), which is defined for each Model$_i$ as: AIC$_i$ – AIC minimum (Akaike, 1992). Models with ΔAIC of 0-2 were considered to have equivalent and substantial empirical support, ΔAIC of 4–7 indicated less support and models with ΔAIC >10 had very low empirical support (Burnham and Anderson, 2002). In order to better interpret the relative likelihood of a model, given the data and the set of candidate models, we used Akaike weights (w$_i$) calculated as described by Burnham (Burnham and Anderson, 2002). Akaike weights provide the weight of evidence in favour of model *i* being the actual best model for the situation at hand, assuming that one of the *N* models tested must be the best model of that set of *N* models. We also computed 95% support regions which were estimated by likelihood profile (Hilborn and Mangel, 1997). All models and numerical algorithms were implemented in C (Borland C++ v.5.01, Borland International Inc., 1996). Finally, we calculated Moran's I autocorrelation coefficient for each species across distance classes for the best model residuals using GS + 5.1.1. (Gamma Design Software, Michigan, USA, 2001) to detect potential patterns of spatial autocorrelation not explained by the models.

3. RESULTS

3.1. Factors influencing tree growth

A number of alternative models differing in complexity and number of factors were evaluated. Model VIII (see Tab. II), which includes an initial size, a competition and a temperature and precipitation related influence on tree growth, resulted in the best fits for all the species (Suppl. Tab. A). Other models, such as models VI and VII had less empirical support while the rest had very low empirical support (see ΔAIC values in Suppl. Tab. A). Comparison between observed growth distributions and predicted growth distributions (given by the best

Table I. Calculated competition indices and description.

Competition index	Index symmetry	Description
$DENS = \sum_{j=1}^{n} j$	Two-sided	Density of all competitor trees j within the plot scaled up to a 1-ha area
$DENShigh = \sum_{\substack{j=1 \\ h_j > h_i}}^{n} j$	One-sided	Density of all competitor trees j within the plot with height h greater than that of the subject tree i and scaled up to a 1-ha area
$BAT = \sum_{j=1}^{n} B_j$	Two-sided	Total basal area B of competitor trees j within the plot scaled up to a 1-ha area
$BAThigh = \sum_{\substack{j=1 \\ h_j > h_i}}^{n} B_j$	One-sided	Total basal area of all competitor trees j within the plot with height h greater than that of the subject tree i and scaled up to a 1-ha area
$relBAT = \sum_{j=1}^{n} \frac{B_j}{B_i}$	Two-sided	Total basal area B of competitor trees j within the plot relative to the total basal area B of subject tree i scaled up to a 1-ha area
$relBAThigh = \sum_{\substack{j=1 \\ h_j > h_i}}^{n} \frac{B_j}{B_i}$	One-sided	Total basal area B of competitor trees j within the plot relative to the total basal area B of the subject tree i considering those competitor trees j with height h greater than that of the subject tree i and scaled up to a 1-ha area

Table II. Functional forms and description of tested models.

Model	Description
Null model. $g = \alpha_1$	Basal growth g is assumed to be constant and independent from any factor. Model parameter is denoted as α_1
I. $g(S) = \alpha_1 + \alpha_2 S$	Basal growth g is defined as a linear function of initial size S. Model parameters are denoted as α_i
II. $g(S) = \frac{\alpha_1 S}{\frac{\alpha_1}{\alpha_2} + S}$	Basal growth g is defined as a Michaelis-Menten function of initial size S. Model parameters are denoted as α_i
III. $g(S) = \alpha_1 (S)^{\alpha_2}$	Basal growth g is defined as a power function of initial size S. Model parameters are denoted as α_i
IV. $g(S, C) = \alpha_1 (S)^{\alpha_2} e^{-\alpha_3 C}$	Basal growth g is defined as a power function of initial size S and an exponential function of competition C. Model parameters are denoted as α_i
V. $g(S, C) = \frac{\alpha_1 (S)^{\alpha_2}}{1 + \alpha_3 C}$	Basal growth g is defined as a power function of initial size S and a hyperbolic function of competition C. Model parameters are denoted as α_i
VI. $g(S, C, T, P) = \frac{\alpha_1 T P (S)^{\alpha_2}}{1 + \alpha_3 C}$	Basal growth g is defined as model V times the product term $\alpha_1 TP$ where T denotes annual mean temperature and P denotes annual mean precipitation. Model parameters are denoted as α_i
VII. $g(S, C, T, P) = \frac{(\alpha_1 T + \alpha_4 P)(S)^{\alpha_2}}{1 + \alpha_3 C}$	Basal growth g is defined as model V times the sum term $\alpha_1 T + \alpha_4 P$ where T denotes annual mean temperature and P denotes annual mean precipitation. Model parameters are denoted as α_i
VIII. $g(S, C, T, P) = \frac{(\alpha_1 T P)}{1 + \alpha_3 C} + \frac{\alpha_4 (S)^{\alpha_2}}{1 + \alpha_3 C}$	Basal growth g is defined as a function similar to model VI with the difference that no interaction between climatic factors (annual mean temperature T and annual mean precipitation P) and initial size S is assumed. Model parameters are denoted as α_i

Model parameters (α_i) can be easily interpreted in biological terms. For example for model VIII, α_1 estimates growth sensitivity to changes in the climatic factors (i.e. simplified as annual mean temperature and annual mean precipitation). Growth sensitivity to competition is estimated by α_3. Finally the combination of α_2 and α_4 estimates the initial size-dependent component in the growth of each species. Thus increasing values of α_i denote increasing dependency on- or sensitivity to the corresponding factor.

model VIII) denoted a good fit of the model to the set of observations for each species (Suppl. Fig. A). Moreover, analyses of residuals showed a balanced pattern with respect to independent factors (Suppl. Fig. B). Moran's I correlograms showed a spatial-independent pattern of best model residuals for *Q. ilex* and *P. pinaster*. In contrast, a spatial-dependent pattern was detected for *Q. pyrenaica* and *P. sylvestris* (Suppl. Fig. C). For the last two species, additional factors accounting for spatial variability due, for example, to altitudinal gradients or patchy distributions should be considered in future studies.

All factors included in model VIII (initial size, competition and climatic factors) significantly (i.e., parameter values for these factors were significantly different from zero) explained individual variation in basal area growth for all the species but *Q. pyrenaica* (Suppl. Tab. A). For this species, the influence of climatic factors (i.e. the product between annual mean

temperature – T – and annual mean precipitation – P –) on basal area growth was not supported by the data (estimation of model VIII's parameter for the effect of climatic factors equalled zero, Suppl. Tab. A); but taking into account initial size and competition did result in a better description of the data.

Further differences among species were found. For example, *relBAT* (see indices' descriptions in Tab. I) was the competition index that resulted in the best fits for *Q. pyrenaica*, *P. sylvestris* and *P. pinaster* while *BAT* was the best predictor of competition for *Q. ilex* (Suppl. Tab. B).

3.2. Interspecific differences along factors

The same model (VIII) and the same competition index (*relBAT*) were used to evaluate interspecific differences in model parameters. Parameter values for each species' best model and 95% confidence intervals are provided in Table III. The species ranking for α_1 (see parameters' descriptions in Tab. II) values was: *P. pinaster* > *P. sylvestris* > *Q. ilex* > *Q. pyrenaica*. The ranking for α_3 was: ((*P. pinaster* ≥ *P. sylvestris*) ≥ *Q. pyrenaica*) > *Q. ilex*. Parameters α_2 and α_4 can only be compared jointly, since their dimensions depend on one another (Fig. 4).

A functional interpretation (see Tab. II for a biological interpretation of models' parameters) of species ranks translates into the following results: *Q. ilex* was the species most tolerant to competition, followed in decreasing order by *Q. pyrenaica*, *P. sylvestris* and *P. pinaster*. However, the latter three species did not differ significantly in their tolerance to competition. *P. pinaster* was the species that exhibited the highest sensitivity to climatic factors, followed in decreasing order by *P. sylvestris*, *Q. ilex* and *Q. pyrenaica*. Given that growth dependency on initial size was defined by two parameters in model VIII, interspecific differences cannot be grasped by a simple linear pattern (Fig. 2). For initial size values lower than 500 cm², *P. sylvestris* was the species with the highest initial size-dependent growth followed by *Q. pyrenaica*, *Q. ilex* and *P. pinaster*. However, initial size-dependent growth changed as initial size increased. For initial size values higher than 500 cm², *Q. pyrenaica* was the species with the highest initial size-dependent growth, followed by *P. sylvestris*, *Q. ilex* and *P. pinaster* (Fig. 2).

3.3. Rank reversals

In general, pines exhibited higher growth than oaks. *P. pinaster* had the highest average growth followed in decreasing order by *P. sylvestris*, *Q. pyrenaica* and *Q. ilex* (Fig. 3) However, tree growth changed depending on initial size, competition intensity and climatic factors, and rank reversals in species growth were observed along variation in each factor (Fig. 4). For example, under xeric conditions (i.e. $T = 14$ °C and $P = 450$ mm) and for low initial size (i.e. 200 cm²), species growth ranking was: *P. sylvestris* > *P. pinaster* > *Q. pyrenaica* > *Q. ilex* (Fig. 4a). For the same xeric conditions
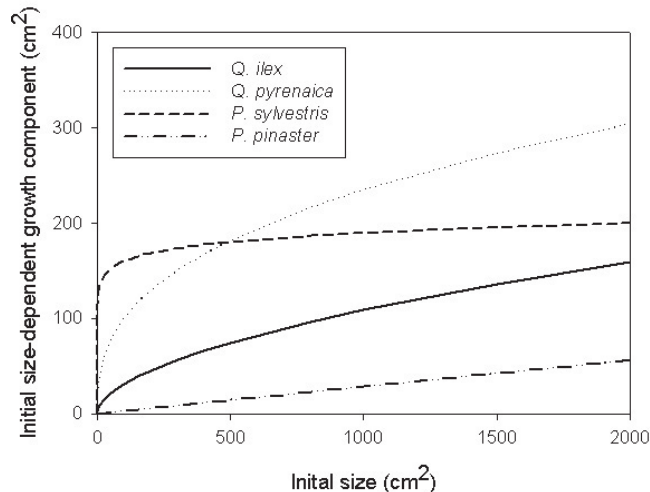

Figure 2. Initial size-dependent growth component for the studied species defined as: $\alpha_4(S)^{\alpha_2}$ where α_i denotes species specific parameters and S denotes initial size. The estimates of parameters α_4 and α_2 for each species were obtained for fitted model VIII with *relBAT* as competition index, according to best model fits.

but higher initial size (i.e. 2000 cm²), however, species ranking changed along the competition gradient and species shifts were observed (Fig. 4b). In particular, *Q. ilex* was the species with the lowest growth rates for values of competition intensity below 500. For competition values between approx 500 and 1300, it ranked second after *Q. pyrenaica*, while for competition values higher than 1300, it ranked first. *Q. pyrenaica* ranked first when competition intensity was lower than approximately 1000. Under mesic conditions (i.e. $T = 7$ °C and $P = 1300$ mm), species growth patterns were similar to those previously mentioned for both low and high initial size (Figs. 4c and 4d). However, for *P. pinaster* and *P. sylvestris* (the most sensitive species to climatic factors), these conditions pushed the lines upwards, which changed species growth ranking for high initial size (Fig. 4d). Under these mesic conditions and for high initial size, *P. pinaster* ranked first when competition intensity was lower than approximately 500. As found for xeric conditions, *Q. ilex* ranked first under high competition intensity.

4. DISCUSSION

4.1. Factors influencing tree growth

Tree size, competition and site variables that reflect different climatic conditions are recognized as key factors influencing tree growth (e.g. Adame et al., 2006; García-Abril et al., 2007; Hein and Dhote, 2006). In this study, tree size and competition were significant factors that explained tree growth for the studied species. Mean temperature and precipitation also influenced tree growth for most of the species. The magnitude of the effect of each factor on tree growth was species dependent, denoting interspecific differences in sensitivity to these

Table III. Maximum likelihood parameter estimates (α_i) and 95% confidence intervals (C. int) for the best-fit models relating basal growth to a number of factors (i.e. annual mean temperature – T –, annual mean precipitation – P –, initial size –S– and competition – C –). That competition index that resulted in the best fit for each species is also indicated.

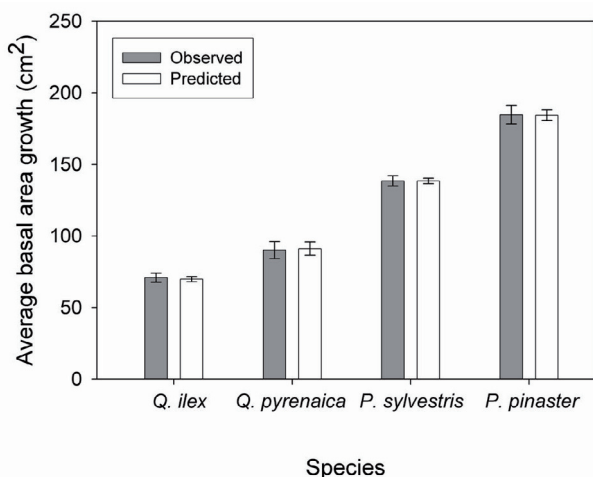|	Best Model	Best C	α_1 (%95 C.int)	α_2 (%95 C.int)	α_3 (%95 C.int)	α_4 (%95 C.int)
Q. ilex	VIII	*BAT*	5.0E-05	0.52	3.4E-06	3.91
			(1.2E-05-6.0E-05)	(0.49-0.54)	(2.4E-06-4.5E-06)	(3.48-4.63)
Q. pyrenaica	VIII	*relBAT*	—	0.37	1.2E-03	18.19
				(0.33-0.47)	(1.0E-03-1.5E-03)	(8.54-23.44)
P. sylvestris	VIII	*relBAT*	1.0E-02	0.07	1.6E-03	114.72
			(3.1E-03-1.7E-02)	(0.02-0.13)	(1.4E-03-1.9E-03)	(57.27-193.80)
P. pinaster	VIII	*relBAT*	3.2E-02	0.98	1.7E-03	0.03
			(2.8E-02-3.5E-02)	(0.62-1.00)	(1.4E-03-2.1E-03)	(0.01-0.05)

Figure 3. Observed and predicted mean basal area growth for the studied species. Error bars denote 95% confidence intervals of the mean.

factors. For *Q. pyrenaica*, tree size and competition but not climatic factors (mean temperature × mean precipitation) were significant determinants explaining most of the variability in growth. The main reason for the lack of influence of climatic factors on *Q. pyrenaica*'s growth may be the narrower range of climatic conditions experienced by this species in the studied region as compared with the rest of species (Figs. 1 and 3). *Q. pyrenaica* is a species that exhibits however, a wider climatic range in other regions of Spain. For instance, in Castile and Leon, *Q. pyrenaica* occupies both Mediterranean and Temperate Submediterranean areas (del Río and Penas, 2006). Further research based on more extensive data sets including different regions are needed to get the whole climatic range of a species which is necessary for accurate predictions and interspecific comparisons at a regional scale.

4.2. Interspecific differences along factors

The higher average growth values exhibited by pines as compared with oaks agree with forestry knowledge in the Iberian Peninsula (Ruiz de la Torre, 2001) and with other studies (Castro-Díez et al., 1998; Pausas et al., 2004; Zavala et al., 2000). Intra-genus differences in average growth also agreed with previous knowledge. For example, marcescent species *Q. pyrenaica* had higher average growth than evergreen *Q. ilex* in agreement with previously reported values for relative growth rate (RGR) of these species (Villar et al., 2004) and the fact that *Q. pyrenaica* occupies more mesic sites that the sclerophyllous *Q. ilex*. With regards to pines, we found the highest average growth in *P. pinaster* which is considered the fastest growing species among pines in the Iberian Peninsula (Ruiz de la Torre, 2001).

It is well known that species differ widely in RGR (Grime and Hunt, 1975). However, the actual growth exhibited by a single individual of a particular species will depend not only on its RGR, but also on the individual's position along the environmental gradient and finally on the individual's sensitivity to the factors defining the environmental gradient.

We found that *Q. ilex* was the species with the lowest sensitivity to competition and with the highest basal growth at high initial size and under high competition intensity of all examined species. This observation agrees with its late successional status (Broncano et al., 1998). *Q. pyrenaica* exhibited less basal growth at high initial size under high competition intensity than *Q. ilex*. However, its growth under such conditions was higher than those of pines (Figs. 4b and 4d) which still agrees with its late successional status (Gómez-Aparicio et al., 2006). In contrast, pines were most hampered in their growth by competition, in agreement with their shade intolerant early successional behaviour (Zavala and Zea, 2004). Pines also exhibited a higher sensitivity to climatic factors than oaks, which might be related to their higher phenotypic plasticity (Sánchez-Gómez et al., 2006a). However, such higher responsiveness to climatic factors did not make pines outperform oaks along the whole climatic gradient. Indeed, species ranking for tree growth changed along gradients of the studied factors. Thus, it cannot be argued that one species grows more than other without referring to a particular setting of environmental conditions.
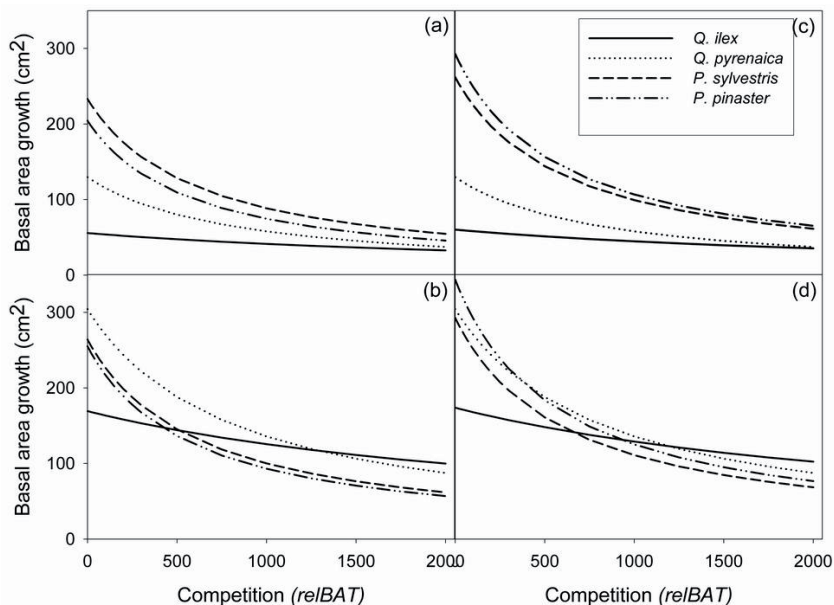
Figure 4. Basal growth against competition intensity. Model VIII and *relBAT* were chosen for comparison among species since they resulted in best model fits. Graph (a) represents values for fixed size of 200 cm^2, annual mean temperature (T) of 14 °C and annual mean precipitation (P) of 450 mm. Graph (b) represents values for fixed size of 2000 cm^2, T of 14 °C and P of 450 mm. Graph (c) represents values for fixed size of 200 cm^2, T of 7 °C and P of 1300 mm. Graph (d) represents values for fixed size of 2000 cm^2, T of 7 °C and P of 1300 m.

4.3. Rank reversals

According to Poorter and Arets (2003), niche differentiation through resource partitioning requires the existence of a trade-off in species performance, in addition to the existence of a resource gradient and a differential species distribution along the gradient. Resource trade-offs can be tested through identification of rank reversals in species performance along the resource gradient (Baraloto et al., 2005). In this study, the axis of competition intensity can be considered as a gradient of resource depletion. The results showed that for early ontogenetic stages (low initial size values), differences between oaks and pines were bigger under mesic than under xeric conditions but no rank reversals were observed. In contrast, for higher initial size values rank reversals were observed. In general, pines performed best under low competition intensity, whilst oaks outperformed pines under high competition intensity. Among oaks, *Q. ilex* was the species with the highest growth under high competition intensity but the lowest growth under low competition intensity.

Several studies focusing on seedlings have failed to test the existence of growth trade-offs (Kitajima, 1994; Veneklaas and Poorter, 1998). The results of this study demonstrate that an appropriate test of trade-offs in species performance along resource gradients need to consider different ontogenetic stages, since expected trade-offs may not operate under early ontogenetic stages but may show up later. The reasons underlying tree performance changes with ontogeny include changes in absolute and relative growth, changes in biomass partitioning patterns and changes in shade and drought tolerance

(Cavender-Bares and Bazzaz, 2000; Sack and Grubb, 2001; Walters et al., 1993).

Another point that needs to be considered is the target variable used to test resource trade-offs. The lack of rank reversals on a growth basis does not imply that niche differentiation might occur through other performance variables. In fact, a previous study on survival revealed rank reversals between pines and oaks along an irradiance gradient at the very early seedling stage (Sánchez-Gómez et al., 2006b). Once different rank reversals and trade-offs at different levels have been identified, a key challenge remains to unveil the relative importance and the role played by these trade-offs and rank reversals in community assembly.

4.4. Implications for forest management and for modelling community structure and dynamics

The results derived from the models developed in this study have important implications for forest management. Two findings are of particular importance: (1) the impact of competition is species dependent and (2) different climatic conditions imply rank reversals in species growth, especially for mature individuals. These findings provide a scientific basis for understanding how management activities such as thinning (e.g. remove old or juvenile individuals, control of thinning intensity, etc.) might contribute to benefit some species at the expense of others under different climatic conditions. They may also contribute to understand species coexistence under future climatic conditions and might help to develop forestry policies and management guidelines for forest biodiversity preservation under climate change.

Advances in analytical forest models (Kohyama, 1994; Zavala et al., 2007) suggest that ecological macroscopic processes such as stand structure and composition can be successfully described as a function of species-level information. Parameterization of species-specific models for growth, survival and recruitment are the first step towards the development of process-based models of forest dynamics that link whole-plant responses to patterns of community organization (Kohyama, 1994). The implementation of analytical models of forest dynamics that predict and explain community structure and dynamics under different disturbance/management regimes seems a feasible goal through a combined program of large scale data analyses, field work and modelling.

4.5. Concluding remarks

We found interspecific differences in tree growth for the four studied species along size, competition and climatic gradients. Species ranking by average growth agreed well with forestry knowledge and previous studies conducted in this region. However, observed rank reversals in species individual growth along gradients of tree size, competition and climatic factors denote the important role of ontogeny and environmental heterogeneity in explaining species-specific growth patterns. From this investigation, we obtain insights into tree growth that are critical for developing process–based models of forest dynamics in this region.

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Online Material

Table A. Maximum likelihood parameter estimates for the models tested relating basal growth with a number of factors (i.e. annual mean temperature – T –, annual mean precipitation – P –, initial size – S – and competition – C–). Model fits are evaluated through differences in AIC (ΔAIC) and Akaike weights (w_i). The competition index used to evaluate the best model was *relBAT*. The shape parameter of the gamma distribution is denoted as n. Model parameters are denoted as α_i. The log-likelihood estimation is denoted as logLike.

	Model (factors)	n	α_1	α_2	α_3	α_4	logLike.	AIC	ΔAIC	w_i
Q. ilex	VIII (S, C,T, P)	1.93	1.6E-03	0.54	3.5E-04	2.55	−11275.2	22560.4	0	2.2E+00
	VII (S, C,T, P)	1.91	0.18	0.47	2.5E-04	3.9E-03	−11276.7	22563.4	3.1	1.7E-01
	VI (S, C,T, P)	1.92	5.5E-04	0.49	2.0E-04		−11277.8	22563.6	3.2	1.6E-01
	V (S, C)	1.90	5.13	0.46	2.9E-04		−11279.5	22567.0	6.6	2.6E-02
	IV (S, C)	1.90	4.59	0.47	1.8E-04		−11282.2	22572.4	12.0	1.7E-03
	III (S)	1.89	3.27	0.52			−11295.5	22597.0	36.7	7.4E-09
	II (S)	1.85	165.17	0.46			−11320.3	22646.7	86.3	1.3E-19
	I (S)	1.80	27.02	0.10			−11348.2	22702.4	142.0	1.0E-31
	null	1.24	70.91				−11859.7	23723.4	1163.1	1.9E-253
Q. pyrenaica	VIII (S, C,T, P)	2.32	0	0.37	1.2E-03	18.19	−5365.4	10740.8	0	1.6E+02
	VI (S, C,T, P)	2.34	2.0E-03	0.37	1.2E-03		−5371.6	10751.3	10.5	5.2E-03
	V (S, C)	2.32	18.47	0.37	1.3E-03		−5373.4	10754.8	14.0	9.1E-04
	IV (S, C)	2.35	11.04	0.43	4.6E-04		−5377.5	10763.0	22.2	1.5E-05
	VII (S, C,T, P)	2.34	1.25	0.37	1.2E-03	6.1E-03	−5376.6	10763.3	22.5	1.3E-05
	III (S)	1.77	1.96	0.68			−5531.8	11069.6	328.8	4.0E-72
	II (S)	1.85	367.02	0.52			−5545.4	11096.8	356.0	4.9E-78
	I (S)	1.67	16.55	0.26			−5571.8	11149.6	408.9	1.6E-89
	null	1.04	90.17				−5879.7	11763.5	1022.7	8.3E-223
P. sylvestris	VIII (S, C,T, P)	2.26	1.0E-02	0.07	1.6E-03	114.72	−25604.2	51236.2	0	8.7E+04
	V (S, C)	2.26	193.43	0.05	1.6E-03		−25616.9	51241.7	23.3	8.7E-06
	VI (S, C,T, P)	2.25	2.9E-02	1.3E-02	1.7E-03		−25618.0	51244.1	25.6	2.8E-06
	VII (S, C,T, P)	2.25	5.99	0.14	1.1E-03	4.7E-02	−25622.1	51254.1	35.7	1.8E-08
	IV (S, C)	2.19	63.82	0.18	4.3E-04		−25671.5	51351.0	132.6	1.6E-29
	III (S)	1.91	10.05	0.43			−26045.2	52096.4	878.0	2.2E-191
	II (S)	1.89	252.44	0.84			−26072.8	52151.5	933.1	2.4E-203
	I (S)	1.85	73.20	0.12			−26125.5	52256.9	1038.5	3.1E-226
	null	1.53	138.45				−26627.0	53258.1	2039.7	0
P. pinaster	VIII (S, C,T, P)	2.25	3.2E-02	0.98	1.7E-03	0.03	−10853.5	21716.9	0	4.4E+00
	VI (S, C,T, P)	2.25	2.7E-02	3.9E-02	1.9E-03		−10856.0	21719.9	3	2.2E-01
	VII (S, C,T, P)	2.26	0	2.0E-02	2.1E-03	0.35	−10859.2	21728.5	11.6	2.5E-03
	V (S, C)	2.20	191.31	0.08	1.7E-03		−10878.0	21764.1	47.1	4.8E-11
	IV (S, C)	2.14	70.46	0.19	4.4E-04		−10910.2	21828.5	111.5	5.0E-25
	III (S)	1.82	14.54	0.40			−11077.5	22161.0	444.1	3.0E-97
	I (S)	1.84	96.68	0.12			−11079.5	22165.1	448.2	3.9E-98
	II (S)	1.77	288.17	1.07			−11113.0	22231.9	515.0	1.2E-112
	null	1.55	184.74				−11256.8	22517.6	800.6	1.2E-174

Table B. Maximum likelihood parameter estimates for the best-fit models relating Basal growth with a number of factors (i.e. annual mean temperature – T –, annual mean precipitation – P –, initial size –S – and competition – C –). All the competition indices studied are evaluated. Model fits are evaluated through differences in AIC (ΔAIC) and Akaike weights (w_i). The shape parameter of the gamma distribution is denoted as n. Model parameters are denoted as α_i. The log-likelihood estimation is denoted as logLike.

|	Best Model	C	n	α_1	α_2	A_3	α_4	logLike.	AIC	Δ AIC	w_i
Q. ilex	VIII	BAT	1.91	5.0E-05	0.52	3.4E-06	3.91	–11271.2	22552.5	0	2.0E+01
		BAThigh	1.92	1.3E-03	0.59	4.3E-06	2.10	–11274.8	22559.5	7.1	2.8E-02
		relBAT	1.93	1.6E-03	0.54	3.5E-04	2.55	–11275.2	22560.4	7.9	1.9E-02
		DENShigh	1.91	9.4E-04	0.55	5.2E-04	2.58	–11278.5	22567.0	14.5	6.8E-04
		relBAThigh	1.90	1.5E-03	0.57	3.9E-04	2.15	–11278.8	22567.6	15.1	5.0E-04
		DENS	1.89	7.1E-04	0.53	2.6E-04	3.05	–11280.3	22570.6	18.2	1.1E-04
Q. pyrenaica	VIII	relBAT	2.32	0	0.37	1.2E-03	18.19	–5365.4	10740.8	0	5.2E+09
		relBAThigh	2.24	2.1E-03	0.51	1.3E-03	5.64	–5387.8	10785.5	44.8	1.9E-10
		DENShigh	2.29	5.5E-04	0.53	1.9E-03	5.85	–5391.4	10792.7	51.9	5.4E-12
		BAT	2.20	0	0.70	8.6E-06	3.28	–5396.4	10802.8	62.1	3.3E-14
		BAThigh	2.14	0	0.63	9.7E-06	3.76	–5412.7	10835.4	94.7	2.7E-21
		DENS	2.12	0	0.56	7.7E-04	5.76	–5418.2	10846.4	105.6	1.2E-23
P. sylvestris	VIII	relBAT	2.26	1.0E-02	0.07	1.6E-03	114.72	–25604.2	51218.4	0	2.8E+42
		relBAThigh	2.17	1.4E-02	0.59	1.1E-03	1.52	–25702.0	51413.9	195.5	3.5E-43
		BAT	2.14	4.6E-03	0.60	4.3E-06	5.98	–25761.3	51532.6	314.2	5.9E-69
		BAThigh	2.09	4.5E-03	0.52	3.7E-06	5.94	–25793.0	51596.1	377.7	9.6E-83
		DENShigh	2.08	7.9E-03	0.49	1.1E-03	4.87	–25834.7	51679.4	461.0	7.9E-101
		DENS	2.01	6.0E-03	0.51	3.4E-04	5.11	–25948.2	51906.5	688.1	3.8E-150
P. pinaster	VIII	relBAT	2.25	3.2E-02	0.98	1.7E-03	0.03	–10853.5	21716.9	0	8.4E+10
		relBAThigh	2.21	2.2E-02	1.00	1.7E-03	0.06	–10878.6	21767.2	50.3	1.2E-11
		BAT	2.15	8.7E-03	0.60	3.5E-06	5.01	–10918.7	21847.5	130.6	4.4E-29
		DENShigh	2.10	1.7E-02	0.78	1.9E-03	0.51	–10930.2	21870.4	153.4	4.9E-34
		BAThigh	2.08	1.2E-02	0.70	4.0E-06	1.43	–10935.6	21881.2	164.3	2.1E-36
		DENS	1.99	1.4E-02	0.73	5.6E-04	0.92	–10996.8	22003.7	286.7	5.5E-63
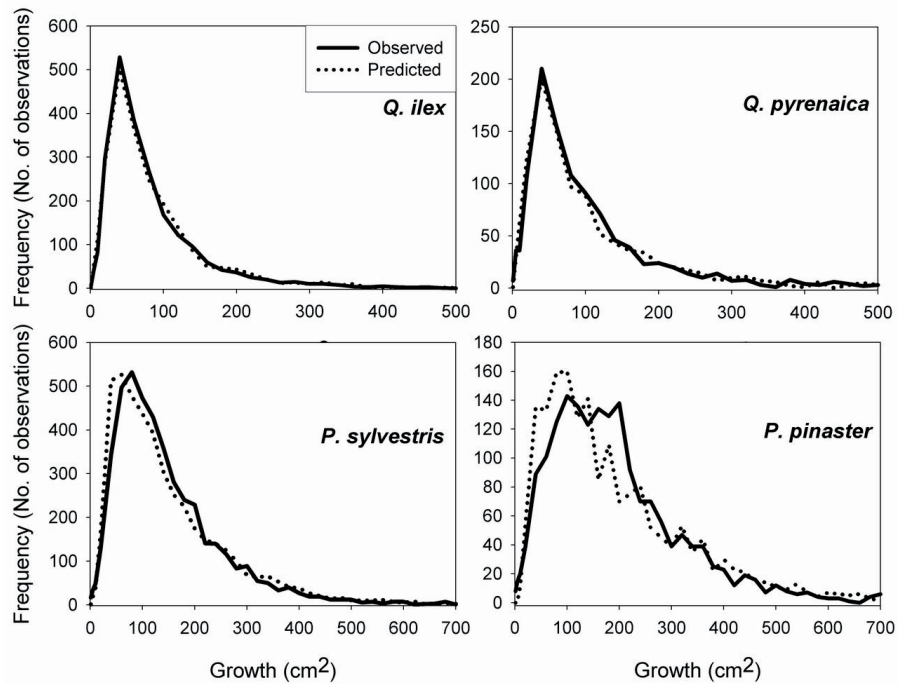
Figure A. Observed versus predicted growth distributions for each species. Predicted values were obtained from the models that resulted in the best fit for each species.
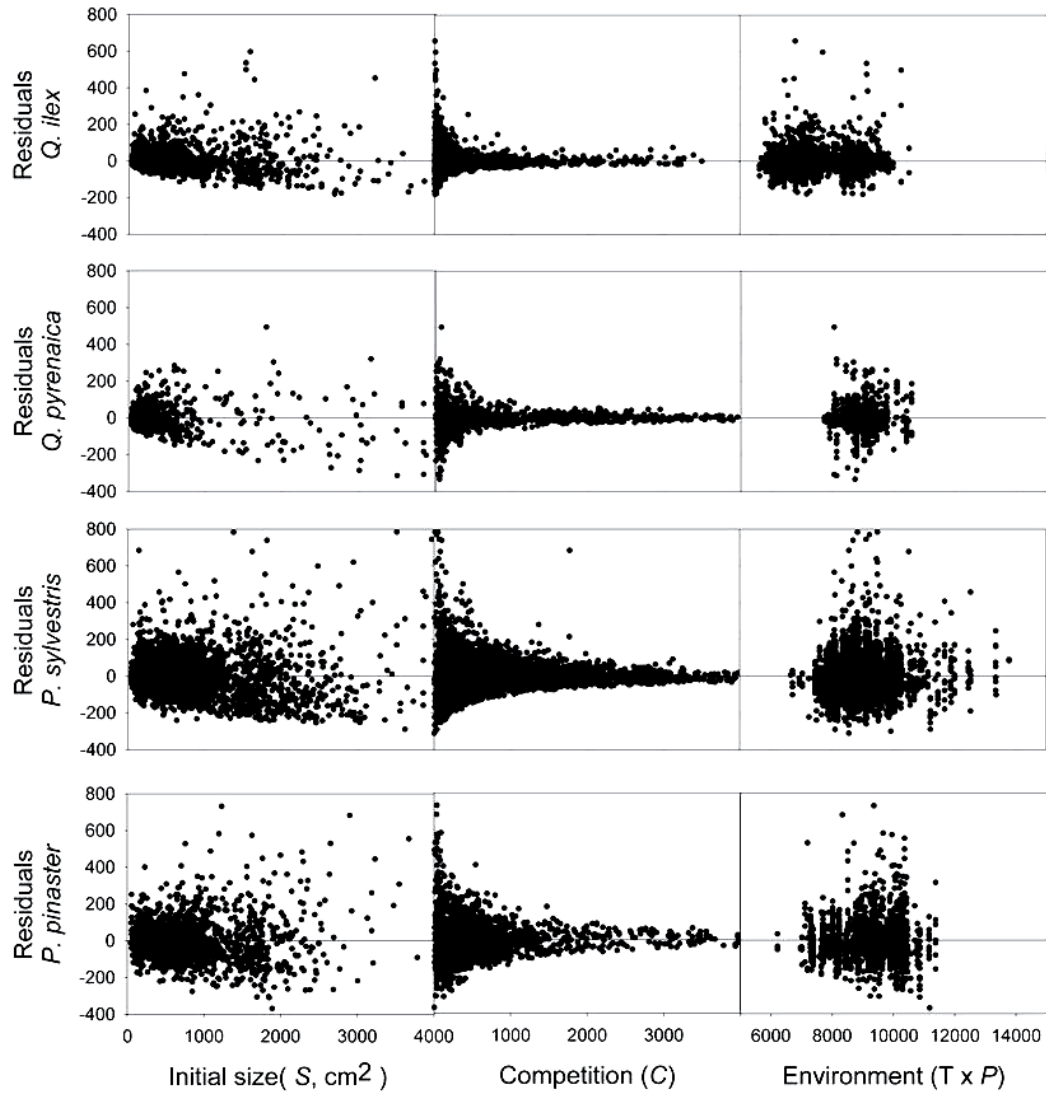
Figure B. Best model residuals against predictive factors for each species. *BAT* was the competition index (*C*) considered for *Q. ilex*, while *rel-BAT* was considered for the rest of species according to best model fits. *T* and *P* denote annual mean temperature and annual mean precipitation respectively.
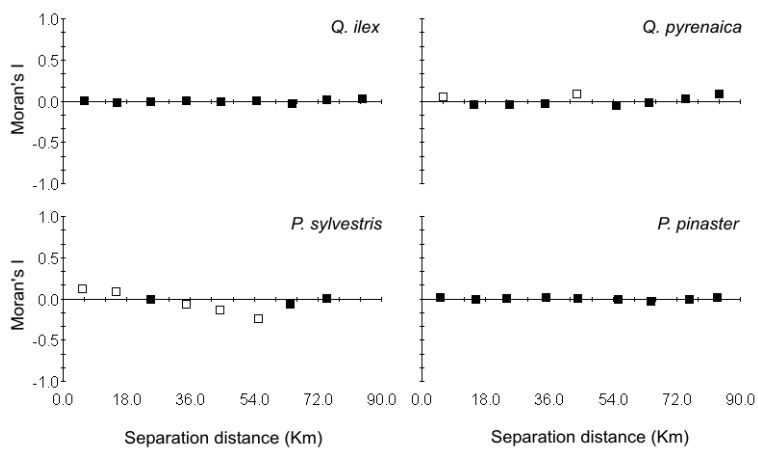
Figure C. Correlograms of Moran's I showing patterns of spatial autocorrelation of best model residuals for the four studied species. Open symbols denote significant Moran's I values for the corresponding distance class. Progressive Bonferroni correction was applied.