



Space–time modeling of changes in the abundance and distribution of tree species



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ABSTRACT

Land use change and global warming are important drivers in the distribution of tree species. The Mediterranean mountain forest ecosystems can be severely affected by climate change since an increment in temperature has been observed. The main aim of this work was to analyze shifts in the distribution and changes in the abundance of Pyrenean oak (*Quercus pyrenaica* Willd.) and Scots pine (*Pinus sylvestris* L.) in Mediterranean mountains over a period of 47 years (1965–2012) by using data from the National Forest Inventories, extending the Universal Kriging/Cokriging models to the space–time case for long-term forest inventory data analysis including climatic variables. Our results indicated that both the distribution and the abundance of Scots pine remained quite constant during the study period. Pyrenean oak increased its presence by 42% whereas its abundance doubled between 1965 and 2012. This movement took place towards both higher and lower altitudes. With regard to climatic factors, the kriging models showed a negative association between the presence of Scots pine and the temperature. However, we found a quadratic relationship between the Pyrenean oak and temperature, pointing to the occurrence of at intermediate altitudes. Additionally, we found significant relationships between the rainfall and the abundance of both species. Rainfall was positively related to the abundance of Scots pine and negatively to that of Pyrenean oak. Our results indicate that there has been a threefold increase in the area covered by mixed stands. However, successive land use changes as well as forest policies related to conservation have played an important role in the distribution of both species and therefore are taken into account in the discussion of these results.

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1. Introduction

Climate change and land use change are the main drivers of global change in ecological ecosystems (Hansen et al., 2001). The effects of both in forest ecosystems are associated with changes in species productivity (Boisvenue and Running, 2006), species distribution (Aitken et al., 2008; Améztegui et al., 2010; Hampe and Petit, 2005; Lenoir et al., 2008), forest dynamics (Kellomäki and Väisänen, 1997; Palombo et al., 2013) and forest disturbances such

as pest outbreaks (Kurz et al., 2008) or forest fires (Brotons et al., 2013; Flannigan et al., 2009), especially in the Mediterranean area (Hódar and Zamora, 2004; Pausas, 2004).

Mountain ecosystems exhibit high biodiversity because many species, often endemic, remain isolated at high elevations (Beniston, 2003). This makes that high mountain systems are particularly vulnerable to climate change (Guisan et al., 1995; Theurillat and Guisan, 2001). Three possibilities exist as regards the fate of mountain forest species in a rapidly changing environment: migration; persistence through adaptation to new conditions in current locations; and extirpation (Aitken et al., 2008; Guisan et al., 1995). During previous periods of climate change, species have tended to respond by migrating rather than adapting to new conditions (Huntley, 1991). Hence, in mountain areas, forest species might migrate upward towards more favorable

Abbreviations: IRWGLS, Iteratively Reweighted Generalized Least Squares; VLS, Variance Least Square; ML, Maximum Likelihood; NFI, National Forest Inventory; SEE, sum of estimations errors; UCK, Universal Cokriging; UK, Universal Kriging; VSEE, variance of the standardized estimation errors.

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ecological niches in response to climate warming (Hughes, 2000; Jump et al., 2009; Lenoir et al., 2008).

In particular, the montane species of the Iberian Peninsula can be especially vulnerable to climate change scenarios (Thuiller et al., 2005). In fact, changes in the distribution of the species have already been detected. Peñuelas and Boada (2003) found that the European beech (*Fagus sylvatica* L.) is occupying the summits of the mountains at the highest altitudes and it is being replaced at mid-altitudes in Northern Spain by the holm oak (*Quercus ilex* L.), which is a more xeritic species. Hernández et al. (2014) demonstrated that both Scots pine (*Pinus sylvestris* L.) and the European beech are shifting towards higher elevations in the Pyrenees. Similarly, Sanz-Elorza et al. (2003) reported movements in shrub species towards higher altitudes over recent decades, mainly associated with changes in climatic conditions. Furthermore, Améztegui et al. (2010) found an expansion in the distribution of mountain pine (*Pinus uncinata* Ram.) in the Pyrenees associated with the land use change (abandonment of rural communities and losses in the primary sector) rather than climate change. The effects of global change on the distribution of species must be understood by forest managers and policy-makers and taken into account in forest management and decision making (Hernández et al., 2014). However, scarce information exists with regard to shifts in species distribution in other mountain areas of the Iberian Peninsula, such as Central Spain.

The broad scale response of species to environmental change has been often assessed by analyzing the distribution of the species (Hernández et al., 2014; Lenoir et al., 2008; Ruiz-Labourdette et al., 2012) since this is easy to measure providing that information is available regarding where a species is present and where it may interact with other species (Ehrlén and Morris, 2015). Nevertheless, the absence/presence data may not provide a complete picture of the shifts in distribution of the species or detect changes in the size of the populations (Joseph et al., 2006). Hence, abundance will be much more useful as an indicator of the carry-on effects that one species will have upon interacting species in the community than presence alone (Ehrlén and Morris, 2015). However, few studies to date have taken into account the abundance of tree species in population trends (Caouette et al., 2015; Ficko et al., 2011).

Alternative data sources have been used to model changes in species distributions, such as forest maps (Benito Garzón et al., 2008), National Forest Inventories (NFIs) (Hernández et al., 2014) or remote sensing techniques such as aerial photographs and satellite images (Blázquez-Casado et al., 2015; Wittmann et al., 2002). NFIs provide estimates of forest resources, growth, mortality, forest health and other valuable information (McRoberts and Tomppo, 2007). Additionally, a large number of species are identified in the NFIs, allowing direct comparisons of species distribution among inventories. Different statistical methods have previously been used to model the distribution and identify the environmental factors that drive this process (reviews in Segurado and Araújo, 2004; Miller et al., 2007; Osborne et al., 2007). Among these approaches, kriging techniques have been found suitable for determining species distribution by spatial interpolation from survey data (Carroll and Pearson, 1998; Hernández et al., 2014). In this study, we take a step further in species distribution modeling by adding the temporal dimension to the Universal Kriging models (Matheron, 1973). These models allow the space–time structure of the variance as well as the effects of climatic and geographical factors to be included in the model. Additionally, these techniques incorporate both spatial and temporal autocorrelation in the kriging prediction, so they are suitable for analyzing survey data when the locations of the samples vary temporally.

The main objective was to analyze shifts in the distribution and changes in the abundance of Scots pine and Pyrenean oak (*Quercus*

pyrenaica Willd.) in Mediterranean mountain over the last 47 years. To achieve this objective we develop species dynamics space–time models integrating NFIs and climate data. These models can be a useful tool in order to understand the past distribution trends of tree species in order to develop forest policies in a global change context. The species studied spread from the lower montane broadleaved forests to the oromediterranean coniferous forest across the altitudinal gradient of the Mediterranean mountains of Central Spain. We hypothesized an upward altitudinal shift of the ecotone between Scots pine and Pyrenean oak that entails an increase in mixed stands. Additionally, we expected an increase in the presence and abundance of the Pyrenean oak and Scots pine.

2. Material and methods

2.1. Study area

This study was conducted in the Central Mountain Range, in Madrid province (Spain). The study area was delimited by 4557N – 4415S and 366E – 469W (UTM, ED50, zone 30N) covering 554,411 ha. The altitude ranged from 430 m asl in the lowest flat-test areas to 2408 m asl in the mountains of the Central Range. The study area in the mountains mainly faces south and south-east. The climate of the region is continental Mediterranean with montane variations and is characterized by a severe summer drought and high seasonal temperature fluctuations. The total rainfall and annual mean temperature are respectively 535 mm and 15 °C in the lowest areas and 1340 mm and 7 °C in the highest areas.

The lower altitudes (<1000 m asl) are mainly dominated by Mediterranean forests of holm oak, and less frequent, stone pine (*Pinus pinea* L.) forest in the South-West. Between 1000 m asl and 1500 m asl sub-Mediterranean forests of Pyrenean oak and pine-woods of Maritime pine (*Pinus pinaster* Ait.) predominate. Scots pine dominates the mountain forests between 1500 m asl and the timberline (2000 m asl). In the transitional areas between the sub-Mediterranean and the mountain conifer belts, Scots pine is mixed with the Pyrenean oak, Maritime pine and black pine (*Pinus nigra* Arnold) (<1700 m asl). Above the timberline, the common juniper (*Juniperus communis* L.), mixtures of broom leguminous bushes and open montane grasslands are the dominant plant communities (Benito Garzón et al., 2008; Cañellas et al., 2000; Franco Múgica et al., 1998; López-Sáez et al., 2014).

The stands of Scots pine have been subjected to long-term forest management and their range have been extended as a result of the forest policy (Franco Múgica et al., 1998; Gil and Aranzazu Prada, 1993). Hence, this species is the widest used in the forestry industry in the study area (CAM, 2012). The main traditional treatment in Pyrenean oak stands, the coppice management, was abandoned during the 1980s due to the decrease in use of firewood and charcoal as an energy source and to rural emigration to the cities (Adame et al., 2008; Cañellas et al., 2004; Gea-Izquierdo et al., 2015; Gonzalez Molina, 1995). To a lesser extent, the Pyrenean oak makes up open woodlands (López Estébanez and Sáez Pombo, 2002).

2.2. Forest inventory data and climate data

We used data from the four existing Spanish NFIs (Table 1; Alberdi Asensio et al., 2010) to evaluate the changes in the spatial distribution of Scots pine and Pyrenean oak. The number of trees per hectare of each species in the plots of the four NFI cycle can be found in Fig. 1. The NFI plots were only installed in woodland areas (i.e. none in non-forested areas). The highest altitude of NFI plots in the study area coincided with the uppermost limit of Scots pine.

Table 1
Year and type of the National Forest Inventory of the plots and number of plots in the study area.

NFI	Year	Type of forest inventory	Number of plots in the study area
First	1965	Relascope	693
Second	1990	Circular plots	1919
Third	2000	Circular plots	1783
Fourth	2012	Circular plots	1182

NFI: National Forest Inventory.

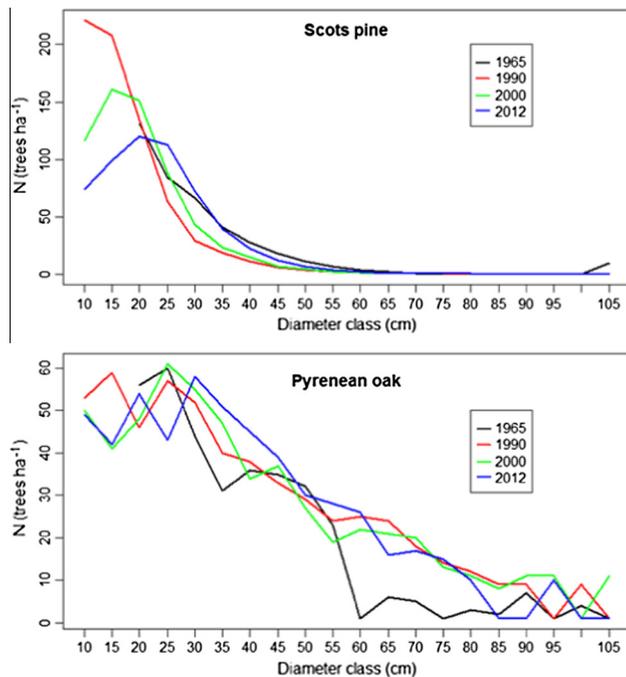


Fig. 1. Number of trees (trees ha⁻¹) of Scots pine (upper) and Pyrenean oak (lower) per diameter class in each inventory.

We used two climatic variables to explain the space–time dynamics of Scots pine and Pyrenean oak: the annual average temperature (temperature, hereafter) and the yearly rainfall (rainfall, hereafter). The annual average temperature and the yearly rainfall are the variables most common used in species distribution models (Porfirio et al., 2014). We obtained the climatic data from the meteorological stations belonging to the Spanish Meteorological Agency (www.aemet.es). We established 1950 as the beginning of the time series and 2014 as last year. The length of the climatic time series differed from one station to another. We used Universal Kriging (UK) with altitude as auxiliary variable to interpolate the temperature and rainfall in the NFI plots in the years of the four NFIs (305 meteorological stations for temperature data and 241 for rainfall data). Additionally, we calculated the annual average temperature and rainfall in the study area using block kriging (Isaaks and Srivastava, 1989) to show the temporal trends of both variables.

2.3. Statistical analysis: space–time models

2.3.1. Distribution (absence/presence) models: Space–time Universal Kriging

Environmental variables such as rainfall, temperature and elevation, as well as ecological processes such as dispersion or mortality, exhibit spatial dependence, some of which are responsible for spatial structure in the distribution of vegetation. Thus, the distribution of vegetation is not random and each observation is not

independent (Miller et al., 2007; Segurado and Araújo, 2004). The spatial autocorrelation must be accounted for in the model because otherwise the risk of Type I errors is increased (Legendre and Legendre, 1998). The Kriging techniques used in this work incorporated spatial and temporal autocorrelation, and deals non-geostationarity through the mean function which depends on the auxiliary variables.

The distribution of the species was evaluated using an indicator variable that took a value 1 if the species was present in the plot and 0 if the species was absent in the plot. We defined a species as present in a given plot when trees, saplings or seedlings were registered in the plot. We used the space–time UK (De Iaco et al., 2002; Montes et al., 2011) to model and map the distribution of Scots pine and the Pyrenean oak in the study area.

$Z(\mathbf{s}, t)$ being as the realization of a space–time random process, the UK model can be expressed as:

$$Z(\mathbf{s}, t) = \sum_{k=0}^p \beta_k f_k(\mathbf{s}, t) + \delta(\mathbf{s}, t) \quad (1)$$

or, in matrix form:

$$Z = X\beta + \delta \quad (2)$$

where $\mathbf{s} \in R^2$ and $t \in T$, $f_k(\mathbf{s}, t)$ are $p + 1$ functions of the auxiliary variables which estimate the space–time mean and $\delta(\mathbf{s}, t)$ is an intrinsically stationary zero-mean residual random process.

The estimation of the optimal weights λ_i involves modeling the variogram. The generalized product-sum model (De Iaco et al., 2002) was used to fit the variogram $\gamma_{st}(h)$:

$$\gamma(h_s, h_t) = \gamma(h_s, 0) + \gamma(0, h_t) - k\gamma(h_s, 0)\gamma(0, h_t) \quad (3)$$

We used a spherical variogram both for the temporal and spatial components assuming a common nugget effect for both components. We used two approaches to simultaneously estimate the variance–covariance matrix $\Sigma(\hat{\theta})$ (which depends on the variogram parameters $\hat{\theta}$) and the β_k coefficients of the auxiliary variables: the Iteratively Reweighted Generalized Least Squares (IRWGLS) (Neuman and Jacobson, 1984) and the Variance Least Square (VLS) (Montes and Ledo, 2010).

We fitted two absence/presence UK models, one for each species. We first used the IRWLS method to fit the models; however, we employed the VLS method when the convergence of the IRWLS could not be achieved. We predicted the distribution of both species at each inventory year in a 500 × 500 m grid covering the study area (22174 points per inventory year). The UK indicator predictions outside [0, 1] were set to the nearest bound, i.e., upward-downward correction (Deutsch and Journel, 1992). Finally, we plotted maps for the dynamics of the mixed and pure stands of both species. We termed ‘pure stands’ those where only one of the two studied species occurred and ‘mixed stands’ those where both species coexisted.

2.3.2. Abundance models: Space–time Universal Cokriging

In order to complete the absence/presence analysis, we modeled the shifts of the distribution of Scots pine and Pyrenean oak over the study period using the basal area (m² ha⁻¹) as response variable. In this case, we used Universal Cokriging models (UCK), extending this technique to the space–time prediction.

Cokriging (Myers, 1982) is an extension of kriging to the case of two or more spatial variables. These variables are not fixed variables that indicate the nature of a trend in the primary variable, but are themselves spatial random variables with expected values and variograms (Gotway and Hartford, 1996). In the space–time UCK the value of the variables can be decomposed into a linear function of the auxiliary variables and a residual process with a

space–time covariance structure defined by the variograms and cross-variograms of the variables:

$$Z_i(s, t) = \sum_{k=0}^p \beta_{ik} f_k(s, t) + \delta_i(s, t) \tag{4}$$

In our study we have two dependent variables ($i = 1, 2$), the basal area of the Scots pine and the basal area of the Pyrenean oak. The UCK prediction $p(Z_1, s_0, t_0)$ of the variable $Z_1(s_0, t_0)$ is a linear combination of the values of this variable in the n sampling points placed in $s_{11} \dots s_{n1}$ and the value of the other variable $Z_2(s_{j2})$ in the m points $s_{12} \dots s_{m2}$:

$$p(Z_1, s_0, t_0) = \sum_{i=1}^n \lambda_{11i} \cdot Z_1(s_i) + \sum_{j=1}^m \lambda_{12j} \cdot Z_2(s_j) \tag{5}$$

and analogously:

$$p(Z_2, s_0, t_0) = \sum_{i=1}^n \lambda_{21i} \cdot Z_1(s_i) + \sum_{j=1}^m \lambda_{22j} \cdot Z_2(s_j) \tag{6}$$

Each variable shows a space–time auto-semivariance function, which is modeled through the variograms γ_{11} and γ_{22} . The cross-variogram characterizes the space–time covariance between each pair of distinct variables (Clark et al., 1989; Cressie, 1993):

$$\gamma_{12}(h) = \frac{1}{2 \cdot N(h)} \sum_{a=1}^{N(h)} (Z_1(u_a, t_a) - Z_2(u_a + h_s, t_a + h_t))^2 \tag{7}$$

The variables Z_1 and Z_2 were standardized to ensure the unbiasedness of the estimators (Deutsch and Journel, 1992). In order to obtain a valid variance–covariance matrix, the variogram and cross-variograms should form a coregionalization model, i.e., each variogram (or cross-variogram) is the linear combination of g spatial or temporal unitary variograms that stand for the different spatial structures i ($i = 1 \dots g$), multiplied by the coregionalization coefficients b_{11i} and b_{22i} , which stand for the contribution of the spatial structure i to the variogram of the variable 1 and 2 respectively, and b_{12i} , which stands for the contribution of the spatial structure i to the cross-variogram.

We included two variograms in the model of coregionalization ($g = 2$): a temporal spherical model and a spatial spherical model,

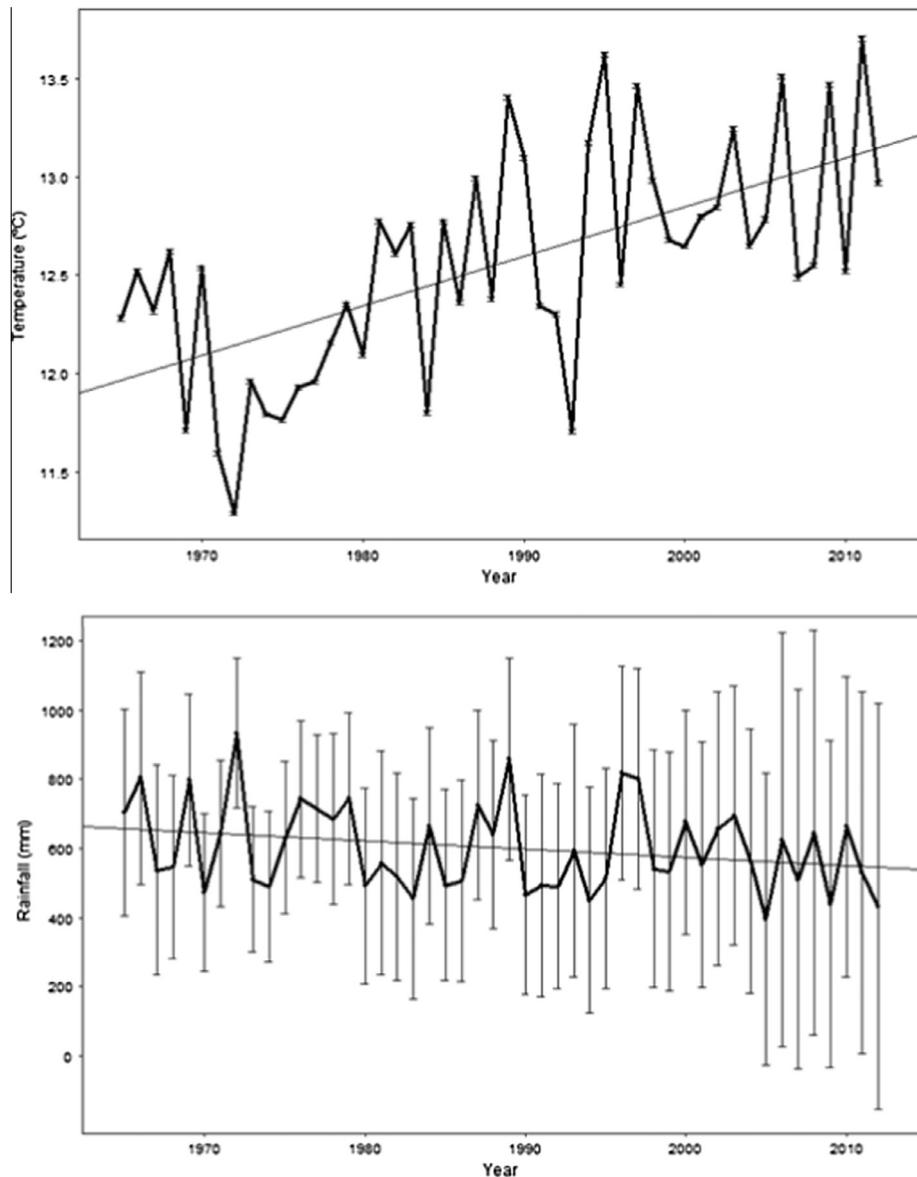


Fig. 2. Annual average values, variance and linear trendline of the temperature (upper) and rainfall (lower) over the study period after the performance of the block kriging.

plus a pure nugget effect variogram that stands for the variance which is neither associated to the auxiliary variables nor to associated to the temporal and spatial structures. The direct and cross variograms are linear combinations of variograms for each structure, that is, the variogram of a given variable is a linear combination of the nugget effect and the temporal and spatial variogram models. The correlogram model parameters (range and b coefficient of each elemental structure) and mean function coefficients β were estimated through IRWGLS, analogously to the UK model.

We assumed that the abundance of one species is not independent of the abundance of the other. Thus, this technique would appear to be useful for modeling the basal area of both species. The basal area of each species was kriged at those prediction points where the presence/absence indicator UK was above 0.5.

2.3.3. Assessment of the statistical significance of the mean function coefficients

The covariance matrix \hat{V} of the generalized least squares estimates $\hat{\beta}$ is obtained as follows:

$$\hat{V} = (X' \hat{\Sigma} X)^{-1} \quad (8)$$

We calculated the standard error estimates $s_k = \sqrt{\hat{v}_{kk}}$ for each beta parameter estimate, $\hat{\beta}_k$, $k = 0, 1, \dots, p$ to construct p -values for significance test of these coefficients based on the t -ratios:

$$t_k = \hat{\beta}_k / s_k, \quad k = 0, 1, \dots, p \quad (9)$$

the degrees of freedom for the t -tests being the difference between the number of observations and the number of auxiliary variables.

2.3.4. Relative structural correlation assessment

We can calculate the relative structural correlation to assess the correlation between the variables associated with each spatial or temporal structure i (Goovaerts and Webster, 1994; Pelletier et al., 2009):

$$\rho_{12i} = \frac{b_{12i}}{\sqrt{b_{11i} \cdot b_{22i}}} \quad (10)$$

In order to quantify the part of the total correlation between variables associated with each structure, we propose the following definition of the relative structural correlation:

$$\rho_{12i}^r = \frac{b_{12i}}{\sqrt{\sum_{j=1}^g b_{11j} \cdot \sum_{j=1}^g b_{22j}}} \quad (11)$$

Positive values of the relative structural correlation indicate positive association between the variables and negative values indicate negative association between the variables.

2.3.5. Model selection: Cross-validation

Cross-validation was used to assess the performance of the UK and UCK model in term of bias and predicted variance. We selected randomly 500 points from data set to carry out the cross-validation of the UK and UCK. The sum of the estimation errors (SEE) was used to check for bias:

$$SEE = \frac{\sum_{i=1}^n (p^*(Z, s_i) - Z(s_i))}{n} \quad (12)$$

where n is the number of observations and $p^*(Z, s_i)$ is the prediction of $Z(s_i)$ leaving out the value observed at s_i . The variance of the standardized estimation errors (VSEE; which should be approximately 1 if the model performed well) was used to check the validity of the prediction error given by the kriging variance:

$$VSEE = \frac{\sum_{i=1}^n (p^*(Z, s_i) - Z(s_i))^2}{\sigma_{UK}^2(s_i) \cdot n} \quad (13)$$

where $\sigma_{UK}^2(s_0)$ is the UK error variance (Cressie, 1993).

The selected space–time UK and space–time UCK models presented SEE values closest to 0 and VSEE values closest to 1. All the statistical analyses were done using a MATLAB R2009a (MATLAB, 2009) package developed by the authors. Maps were created using ArcGis 10.2.2. (ESRI, 2014).

3. Results

3.1. Rainfall and temperature measurements

We employed the VLS method to fit the UK models for the rainfall and temperature. We found significant relationships between both variables and the altitude. As expected, the relationship temperature–altitude was negative and the relationship rainfall–altitude was positive. The spatial correlation was larger for the rainfall (104.16 km) than for temperature (8.67 km), i.e., the rainfall measurements were more constant over the study area than the temperature. Moreover, we found similar temporal ranges of both climatic variables, close to 1 year. Concerning the temporal trends of temperature and rainfall, the block kriging revealed great interannual variations in both variables. In addition, we found a rise in average temperatures and a slight decrease in average rainfall over the study period (Fig. 2).

3.2. Shifts in the absence/presence of Scots pine and Pyrenean oak

The UK model for the Scots pine distribution was fitted using the IRWLS and included the temperature as the auxiliary variable (Table 2). We found a negative relationship between temperature ($p < 0.0001$) and the distribution of Scots pine indicating that this species appeared in the coldest sites of the study area, i.e., at the highest altitudes. Both the temporal and spatial ranges of the Scots pine variogram, 47 years and 136.42 km respectively, were constrained by the fitting procedure to the maximum time difference and distance found in the data set, that is, the semivariance did not stabilize over the study period or the study area. The variance linked to the mean function was 49% (Appendix: Figs. A.1–A.3).

Table 2

Space-time UK models, estimations of the spherical variogram parameters and β coefficients of the auxiliary variables for the Scots pine and Pyrenean oak distributions (absence/presence). The p -values of the auxiliary variables are in brackets.

Parameter	Scots pine (IRWLS)	Pyrenean oak (VLS)
<i>Variogram parameter</i>		
Nugget	0.0600	0.0205
Sill XY	0.0183	0.1160
Range XY	136.3207	2.9682
Sill time	0.0284	0.0044
Range time	47.0000	12.6017
k coefficient	0.1373	0.1060
<i>β coefficients of the auxiliary variables</i>		
β_0	−0.7150 (0.4949)	−0.6348 (0.4953)
Temperature	−0.1358 (<0.0001)	0.2070 (<0.0001)
Temperature ²		−0.0111 (<0.0001)
Rainfall		
<i>Cross-validation statistics</i>		
SEE	−0.0065	0.0027
VSEE	0.9271	1.7776

IRWGLS: Iteratively Reweighted Generalized Least Squares. VLS: Variance Least Square. SEE: Sum of the Estimation Errors. VSEE: Variance of Sum of Estimation Errors.

The space–time autocorrelation explained 44% of the residual variation.

We used the VLS method to fit the UK model for the absence/presence of Pyrenean oak (Table 2). The selected model included the temperature and the square of the temperature with positive and negative β coefficients, respectively, (p -value of both variables < 0.0001) indicating a quadratic relationship between the temperature and the presence of the Pyrenean oak. The negative β coefficient of the square of the temperature indicated that the curve opened downward; the presence of this species reaching a maximum at 9.3 °C. We found a spatial correlation among measurements of 3.0 km and a temporal correlation of 12.6 years. The mean function absorbed 14% of the variance (Appendix: Figs. A.4–A.6) and the space–time autocorrelation explained 63% of the residual variance. Additionally, in this case, the spatial sill was 26 times larger than the temporal sill, indicating larger variability in space than in time.

According to the UK prediction maps (Fig. 3; Appendix: Fig. A.7), the distribution of Scots pine has hardly changed over the study

period. We found that the presence of Scots pine has increased by 11% during the period from 1965 to 2012 (Table 3). The altitudinal range of this species has remained constant over the study period (Table 4).

Furthermore, the UK revealed an expansion of Pyrenean oak in the study area (Table 3). This species increased its distribution by 42% from 1965 to 2012 (Fig. 3; Appendix: Fig. A.7). In contrast to the distribution of Scots pine, the Pyrenean oak expanded its distribution both towards higher elevations and lower elevations, while the average altitude remained constant (Table 4). From 1965 to 2012, Pyrenean oak occupied new areas, creating pure stands (92%) rather than mixed stands (8%). In this respect, we found that there has been a threefold increase in mixed stands over the study period whereas the area occupied by pure stands of Scots pine has reduced by 14% and the area occupied by pure stands of Pyrenean oak has increased by 52%. In this regard, we found an increase in the altitude of the upper limit of the mixed pine–oak stands in 2012 compared to 1965 whereas the increment in altitude was less pronounced at the lower limit (Table 4).

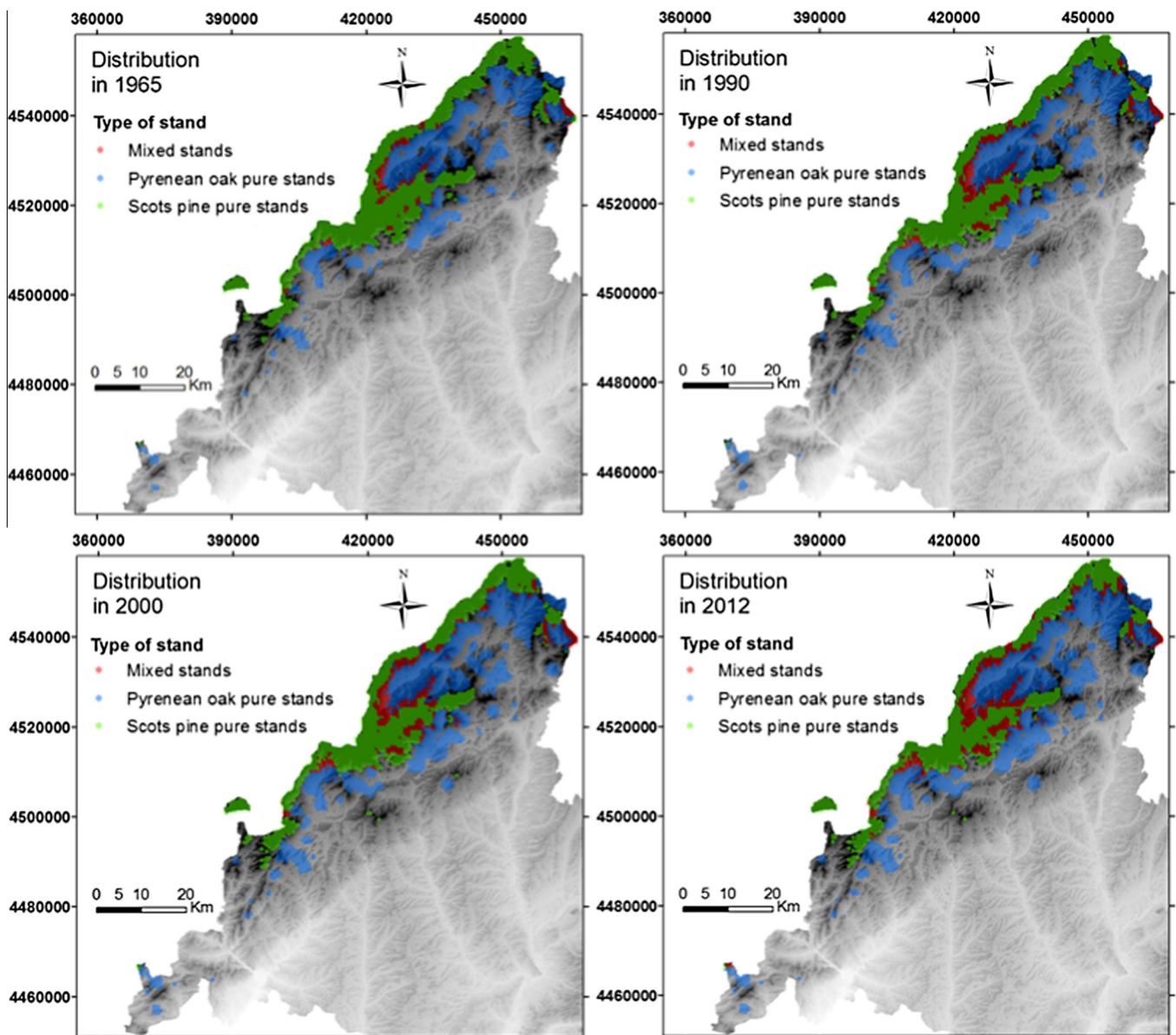


Fig. 3. Distribution (absence/presence) of Scots pine pure stands (green), Pyrenean oak pure stands (blue) and mixed stands (red) in 1965 (upper left), 1990 (upper right), 2000 (lower left) and 2012 (lower right). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Shifts in the abundance of Scots pine and Pyrenean oak

The selected model included rainfall as explanatory variable, presenting a significant association with the basal area of both species (Table 5). The relationship between rainfall and the basal area of Scots pine was positive whereas it was negative in the case of the Pyrenean oak.

The ranges of the spatial and temporal spherical elemental variograms were the maximum distance among plots and the whole study period, respectively (Table 6). We found a positive value of relative structural correlation between the basal area of species in case of the spatial structure, whereas the relative structural correlation was negative for the temporal structure (Table 6, calculated in Eq. (11)). This indicates a positive relationship between the basal area of both species in space and negative in time. Additionally, the absolute value of the relative structural correlation was larger in the time spherical structure than in the spatial one, highlighting that the species abundance for each of the two species has changed oppositely over the successive surveys, although the denser stands of both species tended to coincide geographically.

We found great differences in the basal area of both species. Scots pine always displayed larger basal areas than the Pyrenean oak. The basal area of the Scots pine (Fig. 4) remained quite constant over the study period (18.39 m² ha⁻¹ in 1965, 16.14 m² ha⁻¹ in 1990, 17.81 m² ha⁻¹ in 2000 and 21.32 m² ha⁻¹ in 2012). However, we found a reduction in the number of plots with the lowest basal area whereas the number of plots in the intermediate and uppermost ranges increased from the first NFI to the last (Table 7). The average basal area of the Pyrenean oak increased with time (Fig. 5). Hence, the average basal area of this species in 2012 (4.00 m² ha⁻¹) doubled compared to that in 1965 (1.79 m² ha⁻¹).

4. Discussion

The methods used in these work, space–time UK and UCK, have been shown to be appropriate for monitoring changes in the distributions of forest species using long-term data. The space–time correlation allowed us to use the information from different inventories for data interpolation, thus improving the predictions where the location of the plots varied among inventories. We incorporate the climatic variables in the mean function, which can be interpreted as the climatic potential in basis to the species distribution (derived from the NFI samples over the forest area along the studied period). The spatial and temporal correlation determines the oscillations from this climatic potential in different areas along the period. Three novel approaches used in this work enhanced the model performance and provided a complete framework to understand the relationships between variables: (i) the *p*-values estimation to calculate the significance of the coefficients of the auxiliary variables in the mean function, (ii) the relative structural correlation based on the structural correlations proposed by Goovaerts and Webster (1994) and (iii) the method proposed to determine the part of the variance linked to the mean function

Table 4

Average altitude (m asl) of the prediction points where Scots pine and Pyrenean oak occurred. In brackets, the 5th and the 95th percentiles. Mixed stands are where both species coexist.

Year	Scots pine	Pyrenean oak	Mixed stands
1965	1646 (1343–2040)	1195 (929–1503)	1474 (1264–1722)
1990	1638 (1338–2034)	1211 (929–1582)	1506 (1262–1780)
2000	1619 (1317–2026)	1203 (923–1578)	1490 (1245–1765)
2012	1620 (1322–2024)	1214 (911–1617)	1505 (1272–1783)

Table 5

β coefficients of the auxiliary variables of the space-time UCK model for the basal area of Scots pine and Pyrenean oak and the statistics of the cross-validation. The *p*-values of the auxiliary variables are in brackets.

Basal area of Scots pine		
β_0		-0.1264 (0.4200)
β of the rainfall		0.6111 (<0.0001)
β of the temperature		
β of the temperature ²		
SEE		-0.0250
VSEE		0.9733
Basal area of Pyrenean oak		
β_0		0.3798 (0.2906)
β of the rainfall		-0.4069 (<0.0001)
β of the temperature		
β of the temperature ²		
SEE		-0.0272
VSEE		0.9448

SEE: Sum of the Estimation Errors. VSEE: Variance of Sum of Estimation Errors.

Table 6

Ranges of the elemental variograms, coefficients of the coregionalization model of space-time UCK and relative structural correlations of the elemental variograms.

Elemental variogram	Range	Sills			Relative structural correlation
		Scots pine variogram	Pyrenean oak variogram	Cross-variogram	
Nugget	0.00	0.4652	0.6070	0.6680	0.4588
Spherical XY	136.32	0.2534	0.9417	0.1889	0.1300
Spherical time	47.00	0.5302	0.1485	-0.2806	-0.1927

and the part linked to the space–time autocorrelation, based on Montes and Ledo (2010).

Our findings indicate a relatively steady distribution of Scots pine during the period analyzed in the study area. This is in contrast to the elevation shift of Scots pine towards high mountain grasslands and the reduction in the stands of Scots pine in the Iberian Peninsula predicted by species distribution models as a consequence of climate warming (Benito Garzón et al., 2008; Ruiz-Labourdette et al., 2012). Hernández et al. (2014) found that Scots pine shifted approximately 200 m towards higher elevations but increased its distribution in the Western Pyrenees between 1971 and 2010, stressing the importance of land use changes in species

Table 3

Number of prediction points and proportion, between brackets, of pure stands of Scots pine, pure stands of Pyrenean oak and mixed stands. Mixed stands are where both species coexist. Scots pine and Pyrenean oak are pure stands of these species.

Type of stand	1965	1990	2000	2012
Mixed stand	191 (0.9)	384 (1.7)	471 (2.1)	626 (2.8)
Pyrenean oak stand	1550 (7.0)	1969 (8.9)	2101 (9.5)	2361 (10.6)
Scots pine pure stand	1698 (7.7)	1579 (7.1)	1638 (7.4)	1472 (6.6)
No presence	18,735 (84.5)	18,242 (82.3)	17,964 (81.0)	17,715 (79.9)
Total prediction points	22,174 (100)	22,174 (100)	22,174 (100)	22,174 (100)

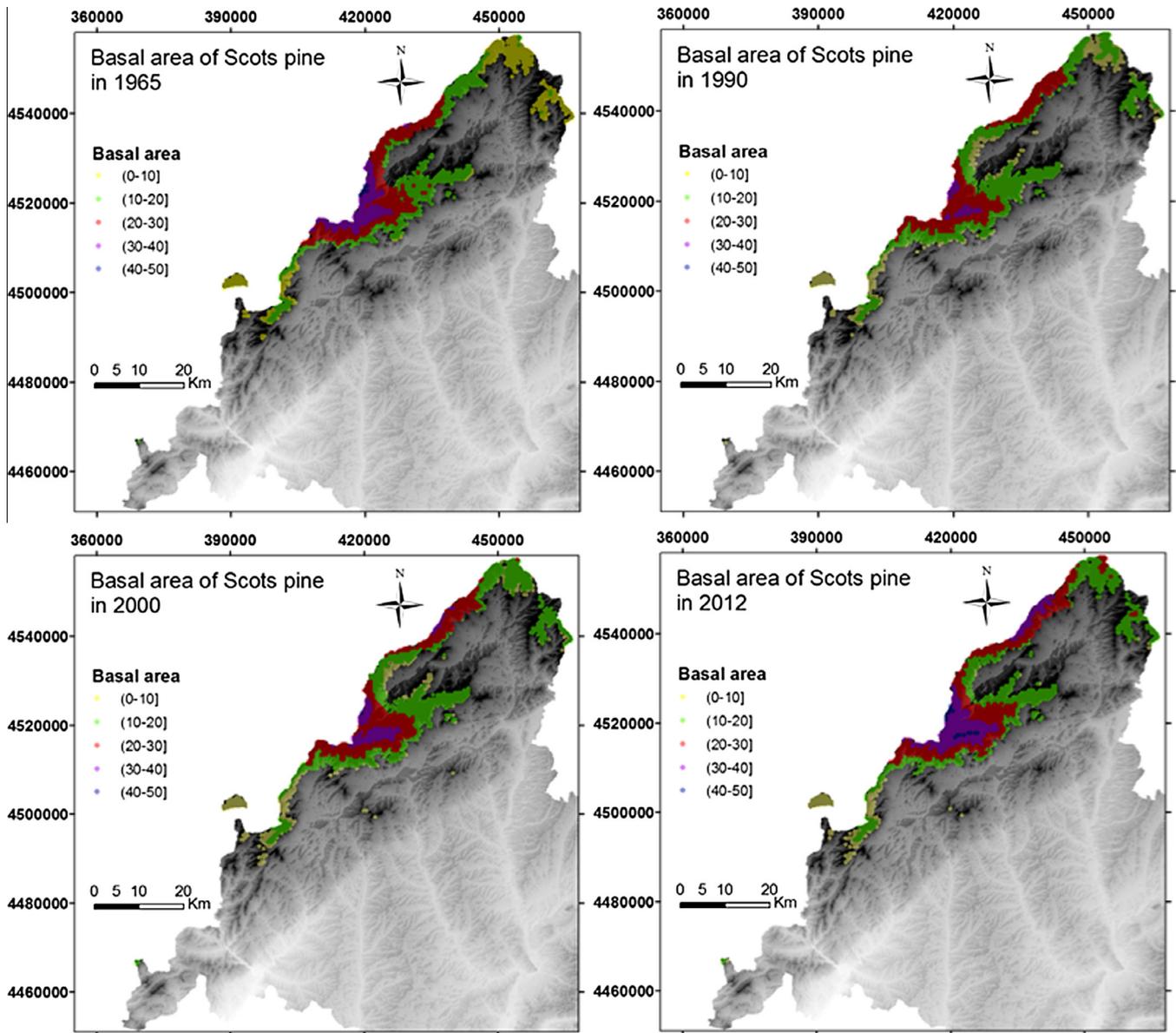


Fig. 4. Basal area of Scots pine in 1965 (upper left), 1990 (upper right), 2000 (lower left) and 2012 (lower right). Yellow: ($0\text{--}10\text{ m}^2\text{ ha}^{-1}$), green: ($10\text{--}20\text{ m}^2\text{ ha}^{-1}$), red: ($20\text{--}30\text{ m}^2\text{ ha}^{-1}$), violet: ($30\text{--}40\text{ m}^2\text{ ha}^{-1}$) and purple: ($40\text{--}50\text{ m}^2\text{ ha}^{-1}$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

dynamics. However, in the study area the shallow and stony terrain impedes the establishment of trees above the tree line. Since the late 20th century, wood production has been reduced towards protective function in those Scots pine stands located at higher altitudes. This may explain the increasing trend in the basal area in the last inventory.

In contrast, the population of Pyrenean oak increased both in presence and abundance. From 1990 (Fig. 1, lower), a large number of trees of this species was incorporated to the upper diameter classes (diameter $> 55\text{ cm}$) entailing the increase in basal area. Ruiz-Labourdette et al. (2012) predicted that the Pyrenean oak would move slightly towards higher elevations. However, our findings indicate that Pyrenean oak range has not shifted to higher elevations (in terms of average altitude) over the last 47 years but rather widen both upwards and downwards. The upwards expansion maybe related to climate factors, but also to changes in forestry policy that favored Scots pine stands over the oak woodlands at the uppermost limit of the Pyrenean oak altitudinal

range at beginning of the 20th century (Cañellas et al., 2000; Sánchez-Palomares et al., 2008). The reduction of firewood exploitation, the conversion of the coppice into high forests, the decrease in human local population, the scarcity of recent large fires in the study area (differently to other Iberian mountains), the protection of Pyrenean oak by the forest policy led to expansion to lower elevation of this species, the increase of the basal area and, the shift of the diameter distribution towards larger sizes (Cañellas et al., 2004; Gea-Izquierdo et al., 2015; Gómez et al., 2003; Pausas, 2004; PORN, 2010).

The area where both species coexist has increased considerably. The Scots pine could facilitate the establishment and development of the Pyrenean oak as occurs with other pine and oak species in southern Spain (Urbieta et al., 2011). The positive spatial correlation between the basal area of both species found in the UCK model indicated that the areas where the basal area of both species is higher coincide. In fact, del Río and Sterba (2009) reported that the competition in mixed stands of Scots pine and Pyrenean oak

Table 7

Number of prediction points placed in each basal area range for the two species studied. The percentage of points in each basal area range is given in brackets.

Basal area range (m ² ha ⁻¹)	1965	1990	2000	2012
<i>Scots pine</i>				
(0–10]	414 (21.9)	383 (19.5)	291 (13.8)	156 (7.4)
(10–20]	679 (36.0)	985 (50.2)	1055 (50.0)	876 (41.8)
(20–30]	575 (30.5)	552 (28.1)	627 (29.7)	702 (33.5)
(30–40]	213 (11.3)	43 (2.2)	135 (6.4)	349 (16.6)
(40–50]	7 (0.4)	0 (0.0)	1 (0.0)	15 (0.7)
Total (0–50]	1888 (100.0)	1963 (100.0)	2109 (100.0)	2098 (100.0)
<i>Pyrenean oak</i>				
(0–4]	1515 (97.7)	1590 (72.4)	1552 (61.4)	1584 (53.5)
(4–8]	16 (1.0)	571 (26.0)	887 (35.1)	1208 (40.8)
(8–12]	19 (1.2)	30 (1.4)	72 (2.8)	144 (4.9)
(12–16]	0 (0.0)	5 (0.2)	18 (0.7)	27 (0.9)
Total (0–16]	1550 (100.0)	2196 (100.0)	2529 (100.0)	2963 (100.0)

is lower than in pure stands and the increase in stocking per occupied area is greater in mixed stands. The areas where both species coexist were mainly areas proximal to the ecotone between the pinewood and the oak woodland: the lowest areas Scots pine range and the uppermost range for Pyrenean oak. Current forestry policy promote mixed stands with complex structures to increase stability and biodiversity (e.g. Spiecker, 2003). Some authors (Gimmi et al., 2010; Ruiz-Labourdette et al., 2012) predict that the Pyrenean oak and other broadleaf species will replace the stands of Scots pine since the increase in the intensity of the summer drought can cause a decrease in the regeneration and recruitment of Scots pine, therefore limiting its distribution (Castro et al., 2004; Fernández-de-Uña et al., 2015; Martínez-Vilalta and Piñol, 2002; Pardos et al., 2007). In addition, a temperature rise may lead to a higher incidence of some outbreaks on pine forests (Hódar and Zamora, 2004). Accordingly, the forecasted increase in temperatures, if not accompanied by an increase in rainfall, will threaten existing populations of Pyrenean oak at lower altitudes (Benito Garzón et al., 2008; de Dios et al., 2009; Gea-Izquierdo et al., 2013; Ruiz-Labourdette et al., 2012). However, despite the climatic trends over the last 47 years (Fig. 2), the Pyrenean oak has expand to lower altitudes as we discussed above.

Concerning the climatic variables, we found that temperature was negatively associated with the presence of Scots pine and rainfall was positively related to its abundance. The quadratic form of the mean function of the Pyrenean oak distribution model indicated that this species occurred at intermediate altitudes in our study area. At lower altitudes (warmer and drier areas), other species such as holm oak are the dominant species whereas Scots pine is established at higher altitudes with colder, more humid conditions (López-Sáez et al., 2014).

It is important not only to monitor the progress of these species but also to study their past and future dynamics in the context of global change in order to develop scientific tools for forest management. In our study area, the long life of these species combined with the changes in use seem to have contributed to the maintenance of Scots pine populations while the distribution range and density of Pyrenean oak as well as the coexistence areas have increased. This is not an equilibrium stage and future changes in the climate may lead to the retraction to the Scots pine with ongoing colonization of the Pyrenean oak (Gea-Izquierdo et al., 2015).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.04.024>.

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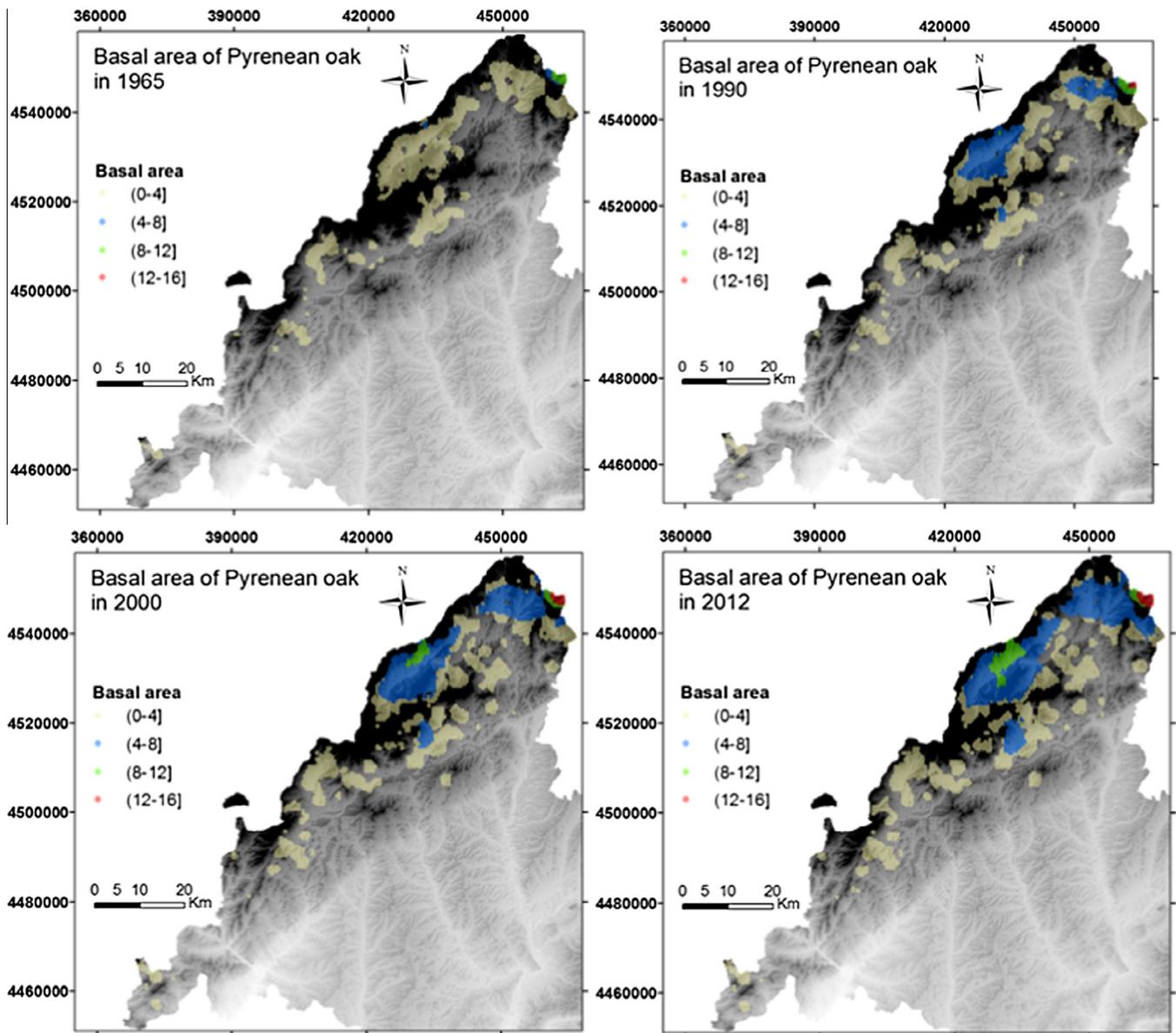


Fig. 5. Basal area of Pyrenean oak in 1965 (upper left), 1990 (upper right), 2000 (lower left) and 2012 (lower right). Yellow: ($0\text{--}4\text{ m}^2\text{ ha}^{-1}$), blue: ($4\text{--}8\text{ m}^2\text{ ha}^{-1}$), green ($8\text{--}12\text{ m}^2\text{ ha}^{-1}$) and red ($12\text{--}16\text{ m}^2\text{ ha}^{-1}$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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