# Effects of climate change on the distribution of Iberian tree species

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### **Abstract**

**Question:** Will the predicted climate changes affect species distribution in the Iberian Peninsula?

Location: Iberian Peninsula (Spain and Portugal).

Methods: We modelled current and future tree distributions as a function of climate, using a computational framework that made use of one machine learning technique, the random forest (RF) algorithm. This algorithm provided good predictions of the current distribution of each species, as shown by the area under the corresponding receiver operating characteristics (ROC) curves. Species turnover, richness and the change in distributions over time to 2080 under four Intergovernmental panel on climate change (IPCC) scenarios were calculated using the species map outputs.

Results and Conclusions: The results show a notable reduction in the potential distribution of the studied species under all the IPCC scenarios, particularly so for mountain conifer species such as *Pinus sylvestris*, *P. uncinata* and *Abies alba*. Temperate species, especially *Fagus sylvatica* and *Quercus petraea*, were also predicted to suffer a reduction in their range; also submediterranean species, especially *Q. pyrenaica*, were predicted to undergo notable decline. In contrast, typically Mediterranean species appeared to be generally more capable of migration, and are therefore likely to be less affected.

**Keywords:** Forest distributions; Iberian Peninsula; Machine learning; Random forest.

**Nomenclature:** Amaral Franco (1990), Govaerts & Avishai (2002) for *Quercus pubescens*.

**Abbreviations:** AUC = Area under curve; CART = Classification and regression trees; IPCC = Intergovernmental Panel on Climate Change; NN = Neural network; RF = Random forest; ROC = Receiver Operating Characteristics.

### Introduction

In recent years, climate change has affected both ecosystems and the organisms that inhabit them (e.g. Walther et al. 2002). Effects of climate change have been estimated at the biome, community and species level (Hansen et al. 2001). One response at the species level involves geographical displacement in altitude and latitude (Hughes 2000); this has been estimated at different scales and in different regions, usually by the use of bioclimate envelope models (Bakkenes et al. 2002; Peterson et al. 2002; Thuiller et al. 2005). Notable displacements have been predicted for all the future climate scenarios studied. However, to date, no studies have been performed on the future of any Mediterranean Peninsular species at any detailed scale. In Europe, the greatest effort has been focused on modelling species presence at the continental scale and at a resolution of 50  $km \times 50 km$  (Bakkenes et al. 2002; Thuiller et al. 2005), using input data taken from the Atlas Florae Europaeae (Jalas & Suominen 1972-1996), although studies more regional in nature have been performed for the United Kingdom (Pearson et al. 2004) and the Swiss Alps (Bolliger et al. 2000).

The impact of global warming is likely to vary from one region to another (McCarthy et al. 2001). High-altitude European ecosystems are expected to be among the most affected by warming (Watson et al. 1997), and high-mountain species will probably be forced to even higher altitudes (where this is possible) (Hughes 2000). However, the Mediterranean Basin is also expected to be seriously affected, because it is an area of transition between the Euro-Siberian or temperate and the Saharo-Sindic climatic regions, and because the problems of drought and forest fires are likely to intensify (Sánchez et al. 2004).

Europe's greatest biodiversity is concentrated in the Mediterranean region (Cowling et al. 1996). The Iberian Peninsula, in particular, is a biodiversity hot spot (Médail & Quézel 1997) but it probably has all the characteristics to render it severely affected by climate change: a large part of it has a mediterranean climate, it has mountainous areas with species at the southernmost limit of their

range, it experiences intense summer drought in some regions, it is geographically isolated (which might hinder the migration of species) and it has a large number of endemics (Gómez-Campo & Malato-Béliz 1985) as well as species whose gene pools differ from those of their European counterparts (Taberlet et al. 1998; Prus-Glowacki et al. 2003).

Climate changes may also affect the composition of ecosystems and biodiversity (Gitay et al. 2002) over time. In a number of regions, species turnover over time has been used to predict changes in future community composition in relation to present diversity (Peterson et al. 2002; Thuiller et al. 2005). Results have generally predicted high turnover in species, and thus in community composition, under possible future climate scenarios.

The forest landscape of the Iberian Peninsula and the expected climate change

The diversity – yet vulnerability – of the habitats of the Iberian Peninsula make it an ideal place for studying the potential displacement and changes in the composition and diversity of forests that might result from climate change.

The forest landscape of the Iberian Peninsula differs from one region to another. In the north (in some cases reaching the mountains in the centre of the Peninsula) forests of temperate broad-leaved species such as Fagus sylvatica, Castanea sativa, Quercus petraea and Q. robur can be found. The Iberian Peninsula represents the southwestern limit of distribution for some of these species, e.g. Q. petraea and Q. robur. At these latitudes, the availability of water is the main factor limiting their survival. The mountains of the north and centre are inhabited by formations of mountain conifers such as Pinus sylvestris, P. uncinata and Abies alba. In the south, occasionally reaching as far as the centre and east of the Peninsula, typical mediterranean species are found such as P. pinaster, P. pinea, P. halepensis, Q. ilex ssp. ilex, Q. ilex ssp. ballota, Q. suber, Q. canariensis and Q. faginea ssp. broteroi; these mountain conifers and sclerophyllous evergreen species are more resistant to the summer droughts that characterize the Mediterranean climate. Sub-Mediterranean formations of Juniperus thurifera, Q. pyrenaica, Q. pubescens, Q. faginea ssp. faginea and P. nigra ssp. salzmannii (i.e. forests of coniferous or deciduous [marcescent] species, or mixtures) are found between the areas occupied by temperate broad-leaved and Mediterranean forests. Future warming and reduced rainfall may affect the vegetation of the Iberian Peninsula (Moreno Rodríguez 2005). The intensification of the summer drought expected in this part of the world (Cubash et al. 1996) could be decisive for certain species.

The aim of the present study was to model the distributions of 20 tree species in the Iberian Peninsula for the years 2020, 2050 and 2080 under one of four different IPCC climatic scenarios associated. Some of the species analysed are either Iberian endemics (e.g. *P. nigra* ssp. *salzmannii*), are genetically different from their European counterparts (e.g. *P. sylvestris*), or are mainly found in the Iberian Peninsula (e.g. *Q. ilex* ssp. *ballota*).

## Methods

All modelling was performed using a bioclimate envelope model (Benito Garzón et al. 2006), employing free software (GRASS GIS (http://grass.itc.it/) (Neteler & Mitasova 2004) for geographic analysis, and the R programme (Anon. 2004) for mathematical analysis and machine learning techniques.

Study area

The study area comprised the Iberian Peninsula (Spain and Portugal), an area geographically isolated from the rest of Europe by the Pyrenees, and from Africa by the Strait of Gibraltar. The study was conducted at a resolution of 1 km<sup>2</sup>, and covered a total of 585 700 km<sup>2</sup>.

# Forest distributions

The present day distributions of the 20 studied tree species (Table 1) were obtained from two maps: the Portuguese forest map (Inventário Florestal Nacional 2001, www.dgrf.min-agricultura.pt/ifn/) (scale 1:1 000 000) and the Spanish forest map (scale 1:200 000) (Ruiz de la Torre et al. 2001). Both were rasterized to a 1-km² grid for analysis. The studied species produce the Peninsula's four main forest formations: temperate broad-leaved forests, mountain conifer forests, sub-mediterranean forests and mediterranean forests.

## Environmental scenarios

The climate scenarios were created taking into account the following variables: mean spring temperature, mean summer temperature, mean autumn temperature, mean winter temperature, spring rainfall, summer rainfall, autumn rainfall, winter rainfall, total annual rainfall, mean annual temperature, mean minimum temperature of the coldest month and mean maximum temperature of the warmest month. These were taken either from meteorological data (for predicting present-day distributions) or from IPCC predictions (for future distribution modelling). Also, two physiographic variables – slope

and aspect (derived from the SRTM V1 elevation model [Shuttle Radar Topographic Mission; Anon. 2006) – were added. Present values for the climatic variables for the Iberian Peninsula were taken from Sánchez Palomares et al. (1999), which covers the period from 1974 to 1990 and which takes into account data from 2605 weather stations. The climatic characterization of Portugal was taken from the AGRIBASE database (AGRIBASE <a href="http://agricultura.isa.utl.pt/agricultura/agribase.htm">http://agricultura.isa.utl.pt/agricultura/agribase.htm</a>); this provides 21 years of data collected by 60 weather stations. These data were interpolated using the thin plane spline method (Mitasova & Mitas 1993).

We simulated the distributions of the major tree species of the Iberian Peninsula as they might be affected by global warming under four climate scenarios – IPCC scenarios A1, A2, B1 and B2 (McCarthy et al. 2001) – and for the time points 2020, 2050 and 2080. To reduce the spatial resolution of these climatic scenarios, each was interpolated using the thin plane spline method (Mitasova & Mitas 1993). Four scenarios were used because climate predictions have been associated with uncertainties in species habitat suitability studies (Thuiller et al. 2005).

The A1 scenario describes economic growth with more efficient technologies and a global population peak in mid-century. A2 describes an increasing global population, with economic growth slower than in the other scenarios. The B1 scenario describes an increasing global population up to 2050 followed by a reduction. Economic development is based on resource-efficient technologies, environmental sustainability and global solutions to economic and social problems. The B2 scenario describes a world focused on local solutions, with an increasing global population (although it increases more slowly than in A2) and intermediate levels of economic development.

# Computational framework

We use a modelling framework (Benito Garzón et al. 2006) capable of using different machine learning techniques (classification and regression trees; CART, RF algorithm and neural networks; NN). We compared these techniques, and chose RF to predict the future distributions of the studied species due to its better performance (see Benito Garzón et al. 2006). Machine learning techniques, which are capable of dealing with complex and non-linear relationships between predictors as well as large amounts of data, are based on automatic pattern detection and the development of knowledge and skills through experience. The RF algorithm (Breiman 2001) improves on CART by conjugating several classifiers.

Within this modelling framework, distributions were predicted for each species and for each climate scenario. The original dataset was randomly split into two: 2/3 of

the total data for the calibration or training dataset and 1/3 for evaluation/validation purposes.

## Algorithm training

For the training of the RF algorithm, we used the R software 'randomForest' library (Liaw & Wiener 2002). The final model was obtained by aggregating 500 base models. The number of variables used at each split (*mtry*) ranged between one and 14.

## Algorithm evaluation

The results provided by RF were evaluated using the evaluation data set (1/3 of the total data), employing the area under the receiver operating curve (AUC, ROC) method (Manel et al. 2001). The ROC curve is a threshold independent measure based on a confusion matrix and plots sensitivity against specificity. The AUC value is the area under the ROC curve. This procedure has been widely used to evaluate models (Fielding & Bell 1997).

## Distribution predictions

This modelling strategy provides probability maps for each species and scenario. To facilitate their interpretation, presence/absence maps were generated from these by maximising the  $\kappa$ -coefficient (Monserud & Leemans 1992).

# Change in species distributions

Using the habitat predictions for each species, the maintenance, expansion or reduction of their ranges with respect to their current potential distributions was quantified for each scenario. The maintained distribution area was calculated from the area occupied at the present time that was also expected to be occupied in the future. Expansion was defined as the area not occupied at present that was likely to be occupied by the species in the future. Contraction was predicted from the area occupied at present but which is probably not to be occupied in the future

Forest turnover, range expansion and contraction, and richness

In this study, we used the potential future distributions to predict species range contraction or expansion, species richness, and species turnover under two different theoretical dispersal scenarios: 'no dispersal' and 'universal dispersal' (see below). Species richness is defined as the sum of the species found per pixel, range contraction as the sum of the lost species per pixel, range expansion as the sum of the gained species per pixel, and species turnover as the net gain or loss of species under

each scenario and dispersal type (Peterson et al. 2002). In this paper, species turnover provides an index of dissimilarity between the present and future compositions of a given area (Peterson et al. 2002), and was calculated for each pixel as follows:

$$TOno = 100*(RC)/(R)$$
 (1)

under the no dispersal assumption (this considers that in the future species can only occupy the places where they are presently found), or

$$TOdisp = 100 * (RE+RC)/(R+RE)$$
 (2)

under the universal dispersal assumption (this considers that species can occupy both the area maintained and new areas in the future, assuming a dispersal of 100%). Where R = species richness; RC = range contraction; RE = range expansion; TO = species turnover.

#### **Results and Discussion**

Algorithm performance

The RF performance was always quite high, with AUC values above 0.93 (Table 1). In the production of presence/absence maps from the probability maps, the  $\kappa$ -coefficient ranged up to 0.5 for each species, which can be considered fair (Monserud & Leemans 1992).

For each species, the simulated area for the present was larger than the actual area (Table 1). Particularly significant were the differences between actual and predicted areas for the species that find their southwestern limits in the Iberian Peninsula (see e.g. Pinus sylvestris). These species distributions are very fragmented as a result of strong competition from other species (as invasive species) and by intense anthropic activity, mainly fire management that has converted land cover from forest to pasture (Garcia Anton et al. 1997). Thus, our models predict the potential current distributions of species based on current climate, and do not account for habitat fragmentation due to human activities and land-use change. In several cases the predicted current ranges are supported by palynological records showing the presence of the species in the near past. Some examples for our model where the predicted area has been

**Table 1.** AUC values obtained for each species. Change in area occupied by the different forest types/species (in km<sup>2</sup> and as a percentage of the potential current area of occupancy) for 2020, 2050 and 2080 under scenario A2. Areas maintained, lost and gained by 2080.

Forests			Present real area	Present (predicted)	A2 2020	A2 2050	A2 2080	A2 2080 Area change		
	Species	AUC	Area (km²)	Area (km²)	Area (km²)	Area (km²)	Area (km²)	Maintained (%)	Increased (%)	Reduced (%)
Mountain conifer forests	A. alba P. sylvestris P. uncinata	0.99 0.98 0.99	183 8254 1129	16786 32288 13896	11319 21629 9809	4811 3907 4005	1574 926 1244	9% 1% 8%	0.4% 2% 0.5%	91% 99% 92%
<b>European</b> forests	C. sativa F. sylvatica Q. petraea Q. robur	0.97 0.98 0.98 0.96	2264 4906 694 3356	52142 36976 27246 56561	45320 24829 12537 44503	44592 7580 2897 33279	27516 2755 908 19148	22% 4% 3% 22%	39% 4% 0.5% 11%	80% 97% 99% 81%
Sub-Mediterranean forests	J. thurifera P. nigra ssp. salzmannii Q. faginea ssp. broteroi Q. canariensis Q. faginea ssp. faginea Q. pubescens Q. pyrenaica	0.98 0.98 0.96 0.99 0.95 0.99	2953 6431 1225 67 5795 775 12232	32267 27418 31949 9454 52766 15639 61728	1976 22250 7647 2300 34799 17721 22421	4290 4858 1858 155 5102 13070 5687	783 465 109 10 563 11309 951	7% 0.04% 0% 0.1% 0.1% 66% 0.5%	2% 2% 0.3% 0.01% 1% 6% 1%	100% 100% 100% 100% 100% 33% 100%
Mediterranean forests	P. halepensis P. pinaster P. pinea Q. ilex ssp. ballota Q. ilex ssp. ilex Q. suber	0.96 0.96 0.96 0.93 0.99	14843 21606 2722 52252 1491 13286	71975 77698 42913 136525 17447 52544	91562 60263 18772 45249 17404 21406	67865 52360 9150 20996 12776 18932	44265 31968 2853 5646 6822 16281	28% 27% 0.5% 2% 13% 5%	32% 16% 6% 2% 26% 26%	73% 75% 100% 98% 99% 96%

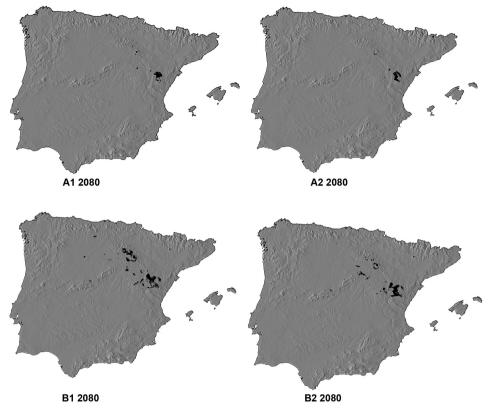


Fig. 1. Potential distribution of Juniperus thurifera (black shaded areas) in 2080 for climate scenarios A1, A2, B1 and B2.

sustained by pollen records are shown in Benito Garzón et al. (2006, 2007).

# Predicted distributions of the different species

As the climate becomes warmer, the temperate broadleaved species can be expected to become relegated to the northern mountains of the Iberian Peninsula, their current range being taken over by sub-mediterranean species. Further, mediterranean species will probably be displaced and occupy areas currently the home of sub-mediterranean species. In our study, scenarios A1 and A2 are those which, in terms of reduction of range, would most affect the studied species, whereas B1 and B2 are less aggressive, at least for 2080 (Fig. 1 shows an example for Juniperus thurifera, a sub-mediterranean species of Ibero -North African distribution). This is to be expected since, in scenarios A1 and A2, a constant increase in CO<sub>2</sub> concentration is predicted up to 2100. For B1 and B2, the increase in CO<sub>2</sub> occurs up to 2050, after which there is a fall and eventual stabilization (Nakicenovic & Swart 2000).

The A2 scenario is expected to be the warmest of the four scenarios used here. Fig. 2 shows an example of the change in the range of the cork oak (*Quercus* suber) over time for scenario A2 (predicted to have the clearest effect on its distribution). This species was predicted to migrate both in altitude and latitude. Table 1 quantitatively records the influence of the A2 scenario on the range of this and other species. Fig. 3 shows the responses of the different species by forest type.

Mountain conifer forests of P. sylvestris, P. uncinata and A. alba

In general terms, these species were predicted to suffer an intense and rapid reduction in their ranges (Fig. 3), especially P. sylvestris (Table 1). P. uncinata and A. alba proved more capable of maintaining their present ranges. They all appeared to show little capacity to expand their range to other areas (Table 1). This drastic and rapid reduction in their distribution was due to the lack of areas of sufficient altitude to which they could find a suitable habitat (with the exception of the higher parts of the Pyrenees). Some of these mountain conifer species – for example, P. sylvestris - have gene pools different from those in the rest of Europe (Prus-Glowacki & Stephan 1994, Prus-Glowacki et al. 2003). Their extinction would therefore lead to a reduction in genetic diversity in the Iberian Peninsula, although they may be expected to survive in northern and central Europe. Studies performed on the future of the Alps suggest that these species will survive at high altitudes (Theurillat & Guisan 2001).

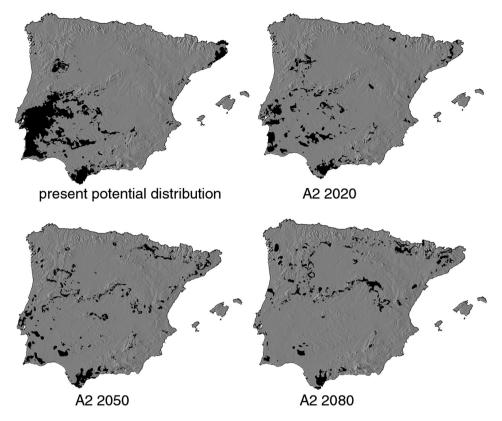


Fig. 2. Potential distribution of *Quercus suber* (black shaded areas) in the present and under the climate projections of scenario A2 (2020, 2050, 2080).

Temperate broad-leaved forests of F. sylvatica, Q. petraea, Q. robur and C. sativa

The area occupied by these typically European forests, which reach their southernmost limit in the Iberian Peninsula, was also greatly reduced. Table 1 shows these species behaved in different ways in 2080 under the conditions of A2. Fagus sylvatica and Q. petraea forests were predicted to occupy smaller overall areas. Quercus robur and C. sativa, however, were not predicted to undergo such drastic decline. Fig. 3 shows the general reduction in the ranges of these deciduous forests. The results suggest that the species of these formations are capable of greater altitudinal displacement than mountain conifer species since they currently inhabit the foothills, valley bottoms and mid-slope areas of mountainsides.

The Iberian populations of the species forming these forests are ecologically and taxonomically unique; their conservation is, therefore, important. The Iberian Peninsula represents the southwestern limit of *Q. robur* and *Q. petraea*, whose populations are endemic subspecies or varieties (*Q. robur* ssp. *estremadurensis*, *Q. orocantabrica*, *Q. petraea* ssp. *huguetiana*).

Sub-Mediterranean forests of Q. pubescens, Q. pyrenaica, Q. faginea ssp. faginea, P. nigra ssp. salzmannii and J. thurifera

The sub-mediterranean regions are located in the transition zones between the mediterranean and the euro-siberian regions. The geographic position and geomorphological characteristics of the Iberian Peninsula favour the existence of these territories, which occupy much of the northern half of the Peninsula, as well as mid-mountain areas. Sub-mediterranean forests are therefore very important in the vegetation landscape of the Peninsula, and are unique in the European context because they are mostly composed of Iberian (P. nigra ssp salzmannii) or Ibero - North African (J. thurifera, Q. faginea and Q. pyrenaica) endemics. In 2080 under the conditions of A2, P. nigra ssp. salzmannii and Q. pyrenaica were predicted to suffer a major decline. The only taxon that did not drastically reduce its area is Q. pubescens, which is the least representative of the sub-Mediterranean species on the Peninsula; it is mainly distributed throughout central and eastern Europe and is only found residually in northern Spain (Sánchez de Dios et al. 2006). This Quercus species inhabits areas that could be less affected by climate change.

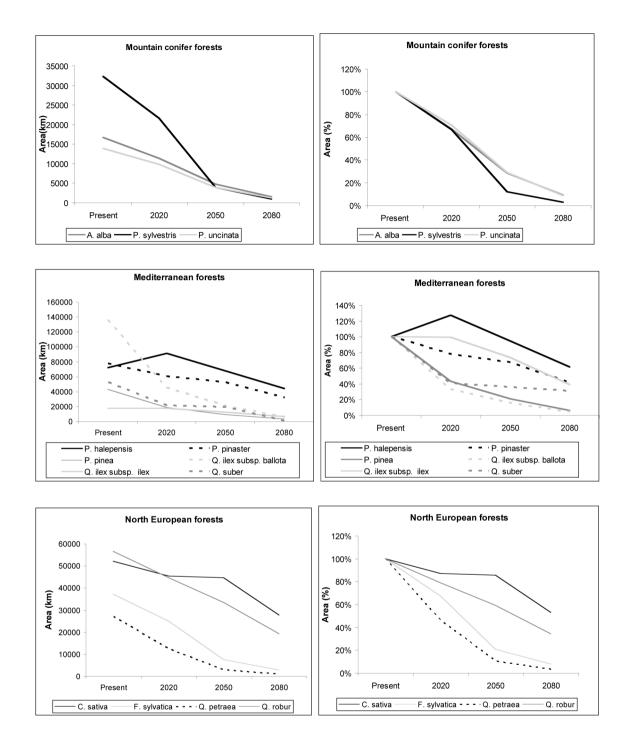


Fig. 3. Area occupied by the different species within forest types for the present conditions and for 2020, 2050 and 2080 under the CSRIO-A2 climate scenarios.

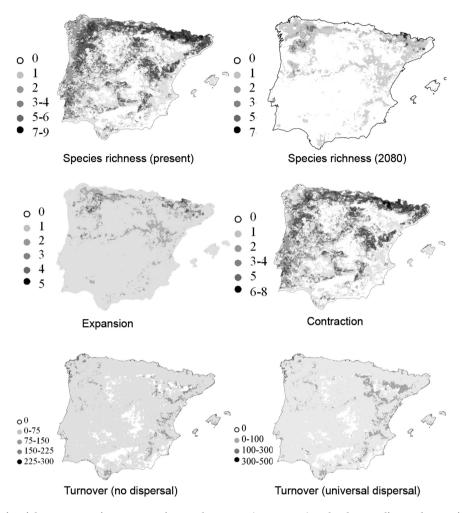


Fig. 4. Species richness, expansions, contractions and turnover (percentage) under the two dispersal scenarios for 2080 CSISO-A2 conditions.

Mediterranean forests of Q. suber, Q. ilex subsp. ilex, Q. ilex subsp ballota, Q. faginea subsp. broteroi, Q. canariensis, P. halepensis, P. pinaster and P. pinea

Forests of mediterranean species generally suffered a smaller overall reduction in area occupied than any other forest type (Table 1, Fig. 3). Despite a loss of present habitat, they will survive if they can colonise similar habitats created by climate change (mainly in areas that are currently sub-mediterranean). The mediterranean species found new climate space in the simulations (P. halepensis, P. pinaster, Q. ilex ssp. Ilex and Q. suber). In 2020, P. halepensis appeared capable of increasing its occupied area, while Q. ilex ssp. ilex underwent little change (Table 1). In contrast, the Q. ilex ssp. ballota was predicted to suffer drastic decline - a tremendous loss since this is one of the most widespread species in Spain. The mediterranean forests were also displaced in altitude and latitude; Fig. 2 shows the change in distribution for Q. suber between the present and 2080.

The loss of mediterranean forests might be set in motion by the aridification predicted by the PROMES project (Moreno Rodríguez 2005). This also predicts that the centre of the Peninsula will become much drier. The species of more continental distribution, such as *Q. ilex* subsp. *ballota*, would be seriously threatened, but those with less continental ranges (*Q. suber*, *Q. ilex* ssp. *ilex*, *P. pinaster* and *P. halepensis*) might be capable of maintaining some of their area, and even of a certain degree of expansion.

Forest turnover, range expansions, range contractions and species richness

The predicted species turnover, range expansion and contraction, and richness values were very similar in all scenarios. Fig. 4 shows the results for Scenario A2 as an example. The highest richness of forest species would be concentrated in mountainous areas in 2080 (Fig. 4). These regions also have the highest contraction

and expansion in their ranges, corroborating the idea of altitudinal movement of the studied taxa. The turnover maps indicate the regions that would be most altered in terms of forest composition in 2080. The northeast of the Peninsula has notably high turnover values. In contrast, the Pyrenees (northeast mountains) show low turnover. High species turnover values have been predicted for Europe (Bakkenes et al. 2002). The species turnovers obtained for the Iberian Peninsula in the present work were always lower, although the work scale was different and therefore comparisons should be made with care.

# Shortcomings of the predictive model

Some intrinsic limitations of predictive models derive from the methods used to measure their accuracy, and from the assumption that the model best calibrated for the present will also be the best for the future. These and other limitations have been discussed in several studies (Schwartz et al. 2001; Pearson & Dawson 2003).

One of the major limitations of our approach is that the entire ecological range of some of the species analysed was not taken into account, although some of the species studied are iberian subpopulations that differ genetically from their European counterparts (Prus-Glowacki & Stephan 1994; Prus-Glowacki et al. 2003; Petit et al. 2005). For some species the northern or southern limits of their distribution were not included because they were not available at the resolution used in this study. Especially interesting are the north african species, since their ranges would be likely to expand northward reaching the Iberian Peninsula. Another limitation is that our models consider only the potential distributions of species as defined by their bioclimate envelopes. Effects on land-use change and other factors on species and forest distributions will be in addition to those covered by our analysis.

#### Main conclusions

This study is the first regional-scale study of the effect of climate change on forest distributions in the Iberian Peninsula to be conducted at high spatial resolution (1 km²). The predicted drastic reduction in the potential ranges of mountain conifer species, the decline of temperate broad-leaved species and the reductions in the areas occupied by mediterranean and sub-mediterranean species, underline the serious potential impact of climate change in the Iberian Peninsula. Since the Iberian Peninsula is a biodiversity hot spot, these reductions in forest cover will also affect European biodiversity.

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#### References

- Anon. (R Development Core Team) 2004. R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.r-project.org/
- Anon. 2006. SRTM Shuttle Radar Topographic Mission http://www2.jpl.nasa.gov/srtm/
- Amaral Franco, J. 1990. *Quercus*. In: Castroviejo, S. (ed.) *Flora Iberica*, pp. 15-36. Real Jardín Botánico de Madrid, CSIC, Madrid.
- Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R. & Latour, B. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Global Change Biology 8: 390-407.
- Benito Garzón, M., Blazek, R., Neteler, M., Sánchez de Dios, R., Sainz Ollero, H. & Furlanello, C. 2006. Machine learning models for predicting species habitat suitability: an example with *Pinus sylvestris* L. for the Iberian Peninsula. *Ecological Modelling* 197: 383-393.
- Benito Garzón, M., Sánchez de Dios, R. & Sainz Ollero, H. 2007. Predictive modelling of tree species distributions on the Iberian Peninsula during the Last Glacial Maximum and Mid-Holocene. *Ecography* 30: 120-134.
- Bolliger, J., Kienast, F. & Zimmermann, N.E. 2000. Risks of global warming on montane and subalpine forests in Switzerland a modeling study. *Regional Environmental Change* 1: 99-111.
- Breiman, L. 2001. Random forest. *Machine learning* 45: 5-32.
- Cowling, R.M., Rundel, P.W., Lamont, B.B. & Arroyo, M.K. 1996. Plant diversity in Mediterranean-climate regions. *Trends in Ecology and Evolution* 11: 362-366.
- Cubash, U., von Storch, H., Wastewitz, J. & Zorita, E. 1996. Estimates of climate change in Southern Europe derived from dynamical climate model output. *Climate Research* 7: 129-149.
- Fielding, A.H. & Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. *Environmental Conservation* 24: 38-49.
- Garcia Anton, M., Franco Mugica, F., Maldonado Ruiz, J., Morla Juaristi, C. & Sainz Ollero, H. 1997. New data concerning the evolution of the vegetation in Lillo Pinewood (Leon, Spain). *Journal of Biogeography* 26: 929-934.
- Gitay, M., Suárez, A., Watson, R.T. & Dokken, D.J. 2002. *Climate change and biodiversity*. IPCC, Geneva, CH.

- Gómez-Campo, C. & Malato-Béliz, J. 1985. *The Iberian Peninsula. Plant conservation in the Mediterranean area.* Junk Publishers, Dordrecht, NL.
- Govaerts, R.H.A. & Avishai, M. 2000. The conserved type of the name *Quercus pubescens* Willd. (Fagaceae). *Taxon* 49: 537.
- Hansen, A.J., Neilson, R.P., Dale, V.H., Flather, C.H., Iverson,
  L.R., Currie, D.J., Shafer, S., Coot, R. & Bartlein, P.J. 2001.
  Global change in forests: Responses of species, communities, and biomes. *BioScience* 51: 765-779.
- Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent. *Trends in Ecology and Evolution* 15: 56-61.
- Jalas, J. & Suominen, J. 1972-1996. Atlas Florae Europaeae. The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki, FI.
- Liaw, A. & Wiener, M. 2002. Classification and regression by randomForest. *The Newspaper of R project* 2/3: 18-22.
- Manel, S., Williams, H.C. & Ormeod, S.J. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38: 921-931.
- McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J. & White, K.S. 2001. *Climate Change 2001: Impacts, adaptation & vulnerability*. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, UK.
- Médail, F. & Quézel, P. 1997. Hot-Spots analysis for conservation of plant biodiversity in the Mediterranean Basin. Annals of the Missouri Botanical Garden 84: 112-127.
- Mitasova, H. & Mitas, L. 1993. Interpolation by regularized spline with tension: Theory and implementation. *Mathematical Geology* 25: 641-655.
- Monserud, R.A. & Leemans, R. 1992. Comparing global vegetation maps with the Kappa statistics. *Ecological Modelling* 62: 275-293.
- Moreno Rodríguez, J.M. 2005. Principales conclusiones de la evaluación preliminar de los impactos en España por efecto del cambio climático. Oficina Española de Cambio Climático. Ministerio de Medio Ambiente, Madrid, ES.
- Nakicenovic, N. & Swart, R. 2000. *Emission cenarios*. Special Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Neteler, M. & Mitasova, H. 2004. Open Source GIS: A GRASS GIS Approach. 2nd. ed. Kluwer Academic Publishers, Dordrecht, NL.
- Pearson, R.G. & Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: arebioclimate envelope models useful? *Global Ecology and Biogeography* 12: 361-371.
- Pearson, R.G., Dawson, T.P. & Liu, C. 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography* 27: 285-298.
- Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R.H. & Stockwell, D.R.B. 2002. Future projections for Mexican faunas under global climate change scenarios. *Nature* 416: 626-629.
- Petit, R.J., Hampe, A. & Cheddadi, R. 2005. Climate changes and tree phylogeography in the Mediterranean. *Taxon* 54:

- 877-885.
- Prasad, A.M., Iverson, L.R. & Liaw, A. 2006. New classification and regression tree techniques: Bagging and random forests for ecological prediction. *Ecosystems* 9: 181-199.
- Prus-Glowacki, W. & Stephan, B.R. 1994. Genetic variation of *Pinus sylvestris* from Spain in relation to other European populations. *Silvae Genetica* 43: 7–14.
- Prus-Glowacki, W., Stephan, B.R., Brujas, E., Alia, R. & Marciniak, A. 2003. Genetic differentiation of autochthonous populations of *Pinus sylvestris* (*Pinaceae*) from the Iberian peninsula. *Plant Systematics and Evolution* 239: 55-66.
- Ruiz de la Torre, J. 2001. Mapa Forestal de España. Escala 1:200.000. ICONA. Ministerio de Agricultura, Pesca y Alimentación, Madrid, ES.
- Sánchez, E., Gallardo, C., Gaertner, M.A., Arribas, A. & Castro, M. 2004. Future climate extreme events in the Mediterranean simulated by a regional climate model: a first approach. *Global and Planetary Change* 44: 163-180.
- Sánchez de Dios, R., Benito Garzón, M. & Sáinz Ollero, H. 2006. Hybrid zones between two European oaks: A plant community approach. *Plant Ecology* 187: 109-125.
- Sánchez Palomares, O., Sánchez Serrano, F. & Carretero Carretero, P. 1999. *Modelos y Cartografía de estimaciones climáticas termopluviométricas para España peninsular.* INIA, Ministerio de Agricultura, Pesca y Alimentación, Madrid FS.
- Schwartz, M.W., Iverson, L.R. & Prasad, A.M. 2001. Predicting the potential future distribution of four tree species in Ohio using current habitat availability and climatic forcing. *Ecosystems* 4: 568-581.
- Taberlet, P., Fumagalli, L., Wust-Saucy, A.-G. & Cossons, J.-F. 1998. Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology* 7: 453-464.
- Theurillat, J.P. & Guisan, A. 2001. Potential impact of climate change on vegetation in the European Alps: A review. *Climatic Change* 50: 77-109.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences* 102: 8245-8250.
- Walther, G.R., Post, E., Convey, P. et al. 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.
- Watson, R.T., Zinyowera, M.C. & Moss, R.H. 1997. The regional impacts of climate change: An assessment of vulnerability. A special report of IPCC Working Group II. Cambridge University Press, Cambridge, UK.

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