ORIGINAL ARTICLE

Forest composition in Mediterranean mountains is projected to shift along the entire elevational gradient under climate change

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ABSTRACT

Aim Species distribution models have been used frequently to assess the effects of climate change on mountain biodiversity. However, the value and accuracy of these assessments have been hampered by the use of low-resolution data for species distributions and climatic conditions. Herein we assess potential changes in the distribution and community composition of tree species in two mountainous regions of Spain under specific scenarios of climate change using data with a high spatial resolution. We also describe potential changes in species distributions and tree communities along the entire elevational gradient.

Location Two mountain ranges in southern Europe: the Central Mountain Range (central west of the Iberian Peninsula), and the Iberian Mountain Range (central east).

Methods We modelled current and future distributions of 15 tree species (Eurosiberian, sub-Mediterranean and Mediterranean species) as functions of climate, lithology and availability of soil water using generalized linear models (logistic regression) and machine learning models (gradient boosting). Using multivariate ordination of a matrix of presence/absence of tree species obtained under two Intergovernmental Panel on Climate Change (IPCC) scenarios (A2 and B2) for two different periods in the future (2041–70 and 2071–2100), we assessed the predicted changes in the composition of tree communities.

Results The models predicted an upward migration of communities of Mediterranean trees to higher elevations and an associated decline in communities of temperate or cold-adapted trees during the 21st century. It was predicted that 80–99% of the area that shows a climate suitable for cold–wet-optimum Eurosiberian coniferous and broad-leaved species will be lost. The largest overall changes were predicted for Mediterranean species found currently at low elevations, such as *Pinus halepensis*, *Pinus pinaster*, *Quercus ilex* ssp. *ballota* and *Juniperus oxycedrus*, with sharp increases in their range of 350%.

Main conclusions It is likely that areas with climatic conditions suitable for cold-adapted species will decrease significantly under climate warming. Large changes in species ranges and forest communities might occur, not only at high elevations within Mediterranean mountains but also along the entire elevational gradient throughout this region, particularly at low and mid-elevations. Mediterranean mountains might lose their key role as refugia for cold-adapted species and thus an important part of their genetic heritage.

Keywords

Climate change, community shifts, gradient boosting, logistic regression, mountain biodiversity, multiple correspondence analysis, Spain, species distribution models.

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INTRODUCTION

Species distribution models (SDMs) are often used to project climate changes in areas that have a climate suitable for the species in question (Thuiller *et al.*, 2005; Diniz-Filho *et al.*, 2009; La Sorte & Jetz, 2010). However, these predictions usually have a coarse spatial grain due to the low resolution of biological and climatic datasets. As a consequence, they cannot identify small patches with suitable conditions that might reduce the negative effects of climate change by providing microrefugia for communities of different species (Pearson, 2006). There is an evident need to develop high-resolution projections to increase our understanding of the effects of climate change on mountain biodiversity (Willis & Bhagwat, 2009). However, few studies to date have implemented this approach (Randin *et al.*, 2009; Engler *et al.*, 2011). High-resolution assessments of the effects of climate change are needed for mountainous regions in particular, because the topographic complexity of such areas means that they usually contain many different habitats and microrefugia in a small area. This characteristic, in combination with factors that are usually excluded in SDMs, such as the availability of water in the soil due to topographical features, plays a significant role in determining the distribution of species in mountainous regions.

Mountains in southern Europe have been recognized as areas of unusually high plant diversity (Väre *et al.*, 2003). Mediterranean mountains have been the site of a significantly high number of speciation events (Martín-Bravo *et al.*, 2010), which have resulted in a high number of endemic species (Gómez-Campo, 1985; Sáinz & Moreno, 2002). It is also likely that European glacial refugia for many plant and animal species were located in the mountains of the Mediterranean Basin, where varied topography resulted in a variety of microclimates that would have provided suitable habitats during both warm and cold periods (Bennett *et al.*, 1991; Taberlet & Cheddadi, 2002). These mountains have acted as refugia for species that flourish in a warm, wet environment during periods of adverse climatic conditions and have sheltered species whose optimum environment is cold and wet since the late-glacial warming (Franco *et al.*, 1998). In fact, in a recent attempt to predict glacial refugia within the Mediterranean Basin, 36% of such refugia were in mountain ranges (Médail & Diadema, 2009). These mountains also constitute the southerly limit or rear edge of the ranges of numerous central European species (Hampe & Petit, 2005). These refugia must have provided suitable habitats for many taxa of the Northern Hemisphere and were the sources for post-glacial recolonization when temperatures rose again at the end of the glacial period (Tzedakis *et al.*, 2002; Médail & Diadema, 2009). Currently, these mountains constitute wet–cool islands of biodiversity in a warm–dry area. These conditions enable plants of Eurosiberian and Boreal origin, as well as elements of the Palaeotropical flora that date from before the establishment of the Mediterranean climate in Europe, to coexist with other xerophyllous species that are adapted to warm summers, when water is scarce (Ruiz-Labourdette *et al.*, 2011). Some of the populations in these mountainous regions are genetically unique. The isolation of these populations has given rise to one of the highest concentrations of endemic species in Europe (Gómez-Campo, 1985; Hewitt, 2000; Sáinz & Moreno, 2002; Väre *et al.*, 2003).

Current predictions of climate change indicate that the highly diverse genetic heritage that exists in the mountains of the Mediterranean will be disturbed significantly in the future (Thuiller *et al.*, 2005). The European Mediterranean region lies in a transition zone between the arid climate of North Africa and the temperate and rainy climate of central Europe. Given this location, even minor changes in atmospheric dynamics can lead to changes in the climate of the Mediterranean Basin (Lionello *et al.*, 2006). In projections of the effects of future climate change, the Mediterranean Basin has been identified as one of the areas that is most vulnerable to the predicted changes (Giorgi, 2006) and is expected to experience greater increases in temperature and aridity than are expected in other regions (Cubash *et al.*, 1996; IPCC, 2007). As a consequence of the aridification of the southern European climate, it is predicted that the mountains of the Mediterranean will become warmer, and will experience less rainfall and more inter-annual variability in temperature and rainfall, than other mountains in Europe (Morales *et al.*, 2005; Gritti *et al.*, 2006; Nogués-Bravo *et al.*, 2007, 2008; Giorgi & Lionello, 2008). In light of these predictions, it is expected that more species will be lost in the Mediterranean mountains than in the Boreal, Alpine and Atlantic regions of Europe as a result of climate change (Thuiller *et al.*, 2005; Bakkenes *et al.*, 2006). This loss of species will be intensified by the isolation of species within a warm, dry matrix at the southern limit of their biogeographical distribution (Petit *et al.*, 2005). Some research indicates that changes in species ranges and community composition are already occurring in these mountains (Granados & Toro, 2000; Goodess & Jones, 2002; Peñuelas & Boada, 2003; Sanz *et al.*, 2003; Sanz-Elorza *et al.*, 2003; Jump *et al.*, 2006; Wilson *et al.*, 2007). Assuming that this is the case, assessment of the effects of future climate change on the diversity and composition of species is of the utmost importance. Some of the species that were analysed in this study do not exist in other southerly regions of Eurasia and constitute an isolated genetic pool (*Pinus sylvestris*, *Fagus sylvatica*) that is discontiguous with the main areas of distribution of these species in the north (Comps *et al.*, 1991; Prus-Glowacki & Stephan, 1994). Other species are endemic (*Pinus nigra* ssp. s*alzmannii*) or have their centres of origin and dispersal in the mountain ranges of the Iberian Peninsula (*Pinus pinaster*) (Gil, 1991).

In the study reported herein, we modelled the distributions of 15 tree species in two connected mountain ranges in the Iberian Peninsula, and projected their potential distributions for two different periods in the future under two climate change scenarios of the Intergovernmental Panel on Climate Change (IPCC). We used data of higher resolution (500 × 500 m) than those used in previous attempts to model forest distributions in the Iberian Peninsula under climate

change (Benito *et al.*, 2008; Keenan *et al.*, 2011). Our data also include information on lithology and the availability of soil water. Specifically, we: (1) assessed changes in potential species distributions using current and future climatic conditions, (2) analysed these changes across the elevational gradient, and (3) evaluated potential changes in the composition of tree communities, all at high spatial resolution.

MATERIALS AND METHODS

We modelled the current and potential distributions of 15 species of trees in mountain ranges of the Iberian Peninsula as functions of climate, lithology and the availability of water in the soil using generalized linear models (GLMs; McCullagh & Nelder, 1989) and data mining models (gradient boosting; Friedman, 1999). Using a multivariate ordination of a matrix of presence/absence of tree species that was obtained for two scenarios of the IPCC Special Report on Emissions Scenarios (SRES), namely A2 and B2 (Nakicenovic & Swart, 2000), for the periods of 2041–70 and 2071–2100, we mapped the principal trends of variation in the composition of current and likely future forest communities within the study area.

Study area

Our study area encompassed a mountainous region of 71,700 km^2 in southern Europe. Its elevation ranged from 900 m to 2592 m a.s.l. The area included two large mountain ranges: the Central Mountain Range, in the central west of the Iberian Peninsula, and the Iberian Mountain Range, in the central east of the peninsula (Fig. 1).

The Iberian Mountains are composed of materials from the Mesozoic (limestones, calcarenites, marls and evaporites from the Cretaceous, dolomites from the Jurassic, and sandstones from the Triassic), with some interspersed sectors that contain metamorphic materials from the Palaeozoic (quartzites, slates, schists and gneisses). In the Central Mountains, there is a predominance of granite and metamorphic materials and a relatively homogeneous siliceous substratum, with the exception of some peripheral and residual areas where Mesozoic limestone is found. On the edges of both mountain ranges, Cenozoic detritic sands can be found. Geological and palaeohistorical data for the region are provided in Gutiérrez-Elorza (1994). The region has one of the highest levels of diversity of flora in the Mediterranean (Castro *et al.*, 1996; Fernández-González *et al.*, 2005). Synopses of the flora and vegetation of the region are provided in Rivas-Martínez (1987), Luceño & Vargas (1991), Costa *et al.* (1998), Mateo (1998) and Ruiz-Labourdette *et al.* (2011).

The composition of the forest in these mountains differs from one region to another. The regions that are wetter during the summer, in the north of the study area, contain forests of temperate broadleaf species (*Fagus sylvatica*, *Quercus petraea*, *Fraxinus excelsior*, *Corylus avellana*, *Betula* spp. and *Pinus uncinata*). The mountain areas that have a more continental climate contain mainly pine forests (*P. sylvestris*, and *P. nigra*
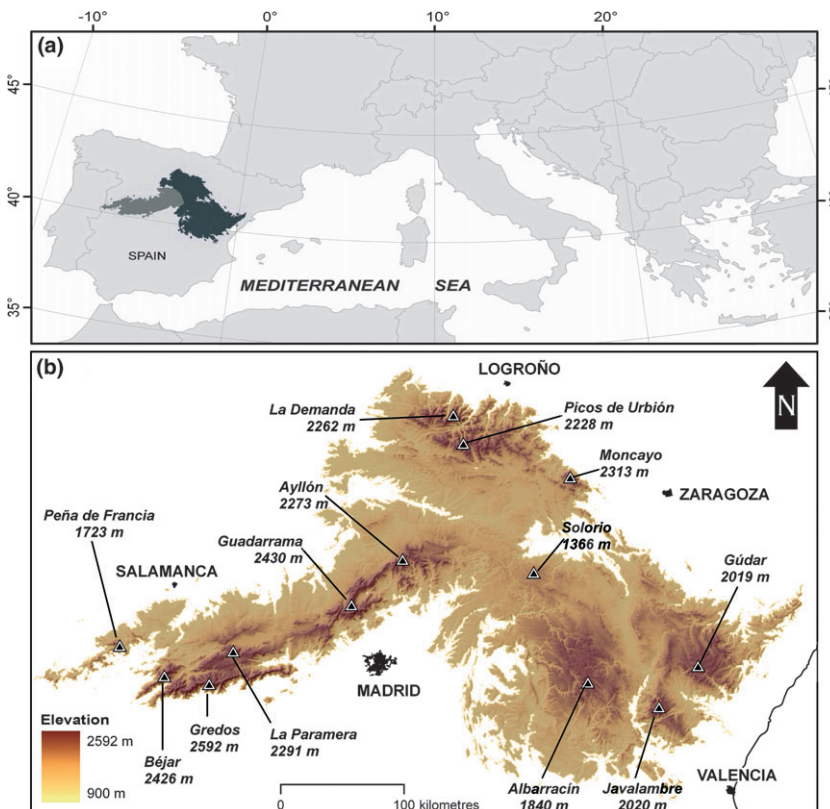
Figure 1 (a) Location of the Central and Iberian Mountain Ranges (light and dark grey, respectively) in the Iberian Peninsula in southern Europe. (b) The elevations of the highest summits in these mountain ranges, together with the main cities in the study area.

ssp. *salzmannii* with *Juniperus communis*). At the lower reaches of these mountainous areas, there are sub-Mediterranean deciduous forests (*Quercus pyrenaica* and *Quercus faginea* in wet, warm areas and forests of *Juniperus thurifera* in dry, cold areas). Wet–warm Mediterranean forests are found in areas that are influenced by the Atlantic Ocean, in the west of the study area, and contain *Quercus suber*, *Castanea sativa* and *Arbutus unedo*. The warmer and drier piedmont environments and the shaded low-elevation mountainous areas contain species that are resilient to summer droughts (*Quercus ilex* ssp. *ballota*, *Pinus halepensis*, *P. pinea*, *P. pinaster* and *Juniperus oxycedrus*).

Bioclimatic data

We used lithology, current climate and hydromorphology of the soil as predictors of the geographical ranges of the species. This set of variables regulates the physiological processes that limit the spatial distribution of plants (Prentice *et al.*, 1992).

Forest species

We collected data from a forest map of Spain at a scale of 1:50,000 (Spanish Ministry of the Environment, 2002). We rasterized the map to a 500×500 m grid format for modelling purposes and created a data matrix of the current presence/absence of tree species in 286,688 cells, which covered the entire study area. Only tree species in the original dataset that were found in more than 5000 cells were modelled.

We included 15 tree species in our study: Eurosiberian coniferous and broad-leaved species (*P. sylvestris*, *J. communis*, *Fagus sylvatica*, *Ilex aquifolium*), sub-Mediterranean gymnosperms (*J. thurifera*, *J. phoenicea*, *P. nigra* ssp. *salzmannii*), sub-Mediterranean semi-deciduous oak species (*Q. faginea*, *Q. pyrenaica*), a sub-Mediterranean phreatophyte (*Fraxinus angustifolia*) and Mediterranean species, which comprised xeric conifers and sclerophyllous evergreen species (*P. halepensis*, *J. oxycedrus*, *Q. ilex* ssp. *ballota*, *P. pinaster*, *P. pinea*). The nomenclature for the tree species is in accordance with Castroviejo (1986–2010).

Lithology and availability of soil water

Lithological data were collected from a geological map of the Iberian Peninsula (Spanish Technological Geomining Institute, 2001). Six lithological classes were distinguished (Table 1). The hydromorphology of the soils provided information on the reduction of the water deficit that might be experienced by the vegetation in the study area during the summer due to an absence of rainfall and high temperatures. As a consequence, hydrophilic and hydrophobic components were incorporated into the models. The calculation of the effects of topography on drainage was based upon the topographic ratio (TR), which captures the degree of hydric convergence/divergence of each 500×500 m cell according to the number of adjacent cells that are located at higher elevations than the cells being

drained. The TR was calculated from the digital elevation model (DEM) SRTM V1 (Shuttle Radar Topographic Mission, at 3 arcsec resolution, *c.* 90 m; Farr *et al.*, 2007) using the ArcGIS software (ESRI, 2009, Redlands, CA, USA) suite with the following formula:

$$TR = \ln A/b \sin \theta \qquad (1)$$

where A is the drained area for a cell (i.e. the upslope contributing area), b is the length of the cell and θ is the angle of the hill slope (Dietrich & Montgomery, 1998). This index has been shown to be correlated well with soil moisture and other hydrological variables (Moore *et al.*, 1991; Taverna *et al.*, 2005).

Climate database

We used 10 climatic variables to model the potential distribution of species: spring rainfall, summer rainfall, autumn rainfall, winter rainfall, total rainfall during the rainy season (autumn, winter and spring), total annual rainfall, mean annual temperature, mean daily maximum temperature (summer), mean daily minimum temperature (winter) and annual thermal oscillation (Table 1).

We calculated these variables from measurements made monthly at a total of 752 rainfall stations and 197 temperature stations that belong to the observation network of the Spanish State Meteorology Agency (AEMET) (Appendix S1 in Supporting Information). From the 1031 rainfall and 440 temperature stations that provide data on this area, we selected the stations with the greatest temporal stability (series length for the baseline period), density (spatial coverage) and homogeneity (Mann test) of time series. The current climate conditions were recorded for the period 1961–90 (Global Standard Climate Normal, World Meteorological Organization).

For the periods 2041–70 and 2071–2100, we used IPCC SRES scenarios A2 and B2 (Nakicenovic & Swart, 2000) with the ECHAM4 atmosphere–ocean general circulation model (GCM) (Max Planck Institute for Meteorology). Scenarios A2 and B2 differ mainly in the amount of carbon predicted to be emitted from energy and industrial sources by 2100. The A2 scenario involves a continuous increase in the human population and semi-intensive use of fossil fuels (an atmospheric CO_2 concentration of 0.70 mg g^{-1} in 2080). Scenario B2 involves slower growth of the human population and lower CO_2 emissions (an atmospheric CO_2 concentration of 0.55 mg g^{-1} in 2080). These global models were downscaled to a regional scale by the Spanish State Meteorology Agency (AEMET, 2008) for the 752 rainfall stations and 197 temperature stations used in our study. Thus, information on current and future climatic conditions was available at the level of individual weather stations. Using these data as a basis, we constructed climatic maps in accordance with the following protocol.

First, we interpolated current and future climate data over the entire study area by using multivariate stepwise regressions that took into account both quantitative geographical data

Table 1 Description of abiotic variables used in the analyses. The geographical factors were used to produce climate maps by means of stepwise multivariate regressions. The climatic cartography obtained was used together with the lithological cartography and the cartography of the hydromorphology of the soils (degree of hydric convergence/divergence) to model the presence/absence of 15 forest tree species by generalized linear models (GLM) and gradient boosting (GB).

Abiotic factors	Variables	Type	Analysis
Geographical			
Elevation	Elevation	Continuous	Stepwise multivariate regression
Slope	Slope	Continuous	of climate variables (climate maps)
Latitude	Distance from the Cantabrian Sea	Continuous	
	Log(distance from Cantabrian Sea)	Continuous	
Longitude	Distance from the Mediterranean Sea	Continuous	
	Log(distance from Mediterranean Sea)	Continuous	
	Distance from the Atlantic Ocean	Continuous	
	Log(distance from the Atlantic Ocean)	Continuous	
Continentality	Distance from the coast	Continuous	
	Log(distance from the coast)	Continuous	
	Hydric distance from the coast	Continuous	
Curvature	Overall curvature	Continuous	
	Plan curvature	Continuous	
	Profile curvature	Continuous	
Aspect	North aspect	Dummy	
	South aspect	Dummy	
	East aspect	Dummy	
	West aspect	Dummy	
Drainage basin	Duero Basin	Dummy	
	Tajo Basin	Dummy	
	Ebro Basin	Dummy	
	Mijares–Turia–Júcar Basin	Dummy	
Climatic			
Rainfall	Spring rain	Continuous	Modelling of presence/absence
	Summer rain	Continuous	of tree species (GLM and GB)
	Autumn rain	Continuous	
	Winter rain	Continuous	
	Autumn, winter and spring rain	Continuous	
	Annual rain	Continuous	
Temperature	Mean annual temperature	Continuous	
	Mean daily maximum temperature (summer)	Continuous	
	Mean daily minimum temperature (winter)	Continuous	
	Annual thermal oscillation*	Continuous	
Lithology	Gneisses (Pre-Hercynian)	Dummy	
	Granitoids (Hercynian)	Dummy	
	Slates and quartzites (Palaeozoic)	Dummy	
	Limestones, dolomites and sandstones (Mesozoic)	Dummy	
	Sands and gravels (Tertiary)	Dummy	
	Sands and gravels (Quaternary)	Dummy	
Hydromorphology of the soils	Hydric convergence index	Continuous	

*Difference between mean daily maximum temperature of the warmest month and mean daily maximum temperature of the coldest month.

(elevation, distance from the coast, latitude, longitude and slope) and qualitative data (drainage basins and aspect), in order to obtain climate maps in a 500 × 500 m grid format (Table 1). Then, we interpolated and mapped the residuals of our climate model and added these to the modelled climatic parameters in order to improve the spatial models for the climatic parameters (see Ninyerola *et al.*, 2007a,b, for a full description of this method).

We calculated the hydromorphology of the soils in the future scenarios by applying the expected increase or decrease in the yearly rainfall volume to the current map of hydromorphology of the soils.

Species distribution models

We used two SDM techniques to generate alternative spatial projections: GLM (McCullagh & Nelder, 1989) and data mining models (gradient boosting; Friedman, 1999). ArcGIS 9.3 (ESRI, 2009, Redlands, CA, USA) was used for spatial analysis and STATISTICA 9 (StatSoft, 2009, Tulsa, OK, USA)

and xlstat 2010 (Addinsof, 2010, New York, NY, USA) for statistical analysis.

Machine learning methods can be applied to large datasets and can deal with nonlinear relationships between variables (Recknagel, 2001). The gradient-boosting tree algorithm that was applied in this study (Friedman, 1999) is a machine learning method that gives more accurate results than other techniques, such as random forest, bagging or single tree approaches (Bühlmann & Hothorn, 2007). The gradient-boosting tree algorithm optimizes the classical classification and regression tree (CART) approach by incorporating bootstrap aggregation of multiple trees (Segurado & Araújo, 2004). The trees that are used are obtained from iteratively reweighted versions of the training data. Finally, the algorithm classifies the cells by weighted majority voting. The GLM that was applied in this study was binomial with logistic regression. A stepwise procedure using Akaike's information criterion (AIC) was used to select the most significant variables for both types of model.

To validate the performance of our models, the original dataset was split randomly into two: two-thirds of the total data were used for calibration (training subset) and one-third to evaluate and validate the models (validation subset). From the training subset, we obtained two probability maps for each species, one using the GLM approach and the other using the gradient boosting technique. We generated binary presence/absence maps from the probability maps by using a threshold to maximize the kappa statistic (Monserud & Leemans, 1992; Benito et al., 2006). Kappa is calculated from the confusion matrix formed by true-positive, false-positive, true-negative and false-negative predictions. The kappa value defines the similarity between the binary map and the available biological evidence. We chose between the models obtained by GLM and gradient boosting on the basis of the value of kappa that was obtained with the validation subset, and selected the model that best explained the current species distribution. To validate the models, we adopted the criteria used by Monserud & Leemans (1992) and assumed that we could model only species with a kappa ≥ 0.4 in one of the two possible models (acceptable degree of similarity). Finally, the model that was selected and validated for each species was applied to the future abiotic scenarios.

Composition of forest species (multiple correspondence analysis)

Using the results of the models as a basis, we designed a presence/absence matrix for all the species in the five scenarios considered: current; B2 for 2041–70; A2 for 2041–70; B2 for 2071–2100; and A2 for 2071–2100. This data matrix was analysed by multiple correspondence analysis (MCA) using the xlstat 2010 package (Addinsof, 2010) to identify the principal trends in the variation of the current and future compositions of species. We determined current and future compositions of forest (community maps) by segmenting the first axis of the MCA (principal variation trend) into roughly equal intervals

that were based upon the coordinates of the cells represented on the first axis (De Aranzabal et al., 2008).

RESULTS

Modelled distributions of forest species

Twelve of the 15 species that were analysed gave acceptable values of kappa ($\kappa > 0.4$; Table 2). In most cases, the gradient-boosting model was selected (eight species), and only four species were modelled with GLM. The presence/absence maps for the five different abiotic scenarios are shown in Appendix S2. The contribution of the abiotic variables to the models is shown in Appendix S3.

The largest changes were predicted for Mediterranean species, namely xeric conifers and sclerophyllous evergreen species, which are tolerant of high temperatures and summertime drought (P. halepensis, J. oxycedrus, Q. ilex ssp. ballota, P. pinaster). Sharp increases were predicted in the range of these species, of the order of 350%, under scenario A2, which is associated with the most severe changes in human population and CO_2 levels. These increases in range only occurred in regions in which the elevation did not differ greatly from that of the original range, which implied that these species could spread from their present positions to successfully colonize flat piedmont and low-elevation mountainous areas.

In contrast, the greatest decreases in range were predicted for the Eurosiberian coniferous and broad-leaved species (Fagus sylvatica, P. sylvestris, J. communis), whose optimum conditions are cold and wet. This decrease ranged from 80 to 99% depending upon the scenario.

These Eurosiberian species are predicted to undergo the biggest elevational displacement among the species that were analysed, with suitable areas being displaced upwards between 200 and 550 m. As a consequence, the tree line would rise and currently treeless areas that are occupied by high-mountain grasslands would be colonized. In our study area, these species may well undergo clear latitudinal displacement towards the north and a large reduction in range. In addition, it is likely that areas with climatic conditions suitable for their survival would disappear from the central and southern massifs.

The models predicted that the geographical ranges of sub-Mediterranean species, such as Q. faginea and Q. pyrenaica (semi-deciduous oak forests), J. thurifera and P. nigra ssp. salzmannii (sub-Mediterranean gymnosperms) and Fraxinus angustifolia (a sub-Mediterranean phreatophyte), would be maintained or decrease somewhat under the different scenarios (losses in area of between 5 and 70%). It is likely that environmental conditions that are suitable for the growth of these species would occur at slightly higher elevations than at present. This increase in elevation (of between 25 and 230 m, depending upon the scenario) would compensate for the warming and water deficit that would be experienced.

The extent of the projected changes in the size of ranges showed a marked relationship with elevation, with the

Table 2 Kappa values obtained for each tree species in the generalized linear model (GLM) and gradient-boosting (GB) models. Text in bold represents the model that was selected finally and used to calculate the presence/absence maps shown in Appendix S2. The table shows the current and predicted area and mean elevation of each species and expected increase in area (%) and in elevation (m) under climate change scenarios A2 for 2041–70, A2 for 2071–2100, B2 for 2041–70 and B2 for 2071–2100 in relation to the current predicted scenario.

| | Kappa | | | | Current | | A2 SCENARIO | | B2 SCENARIO | |
Species	GB	GLM		Current (real)	(predicted)		2041–70	2071–2100	2041–70	2071–2100
Fagus sylvatica	**0.69**	0.59	Area	1746 km^2	3720 km^2		−88%	−99%	−85%	−95%
			Elev.	1333 m	1369 m		+304 m	+547 m	+280 m	+389 m
Fraxinus angustifolia	**0.46**	0.13	Area	1915 km^2	5457 km^2		−16%	−58%	−5%	−36%
			Elev.	1048 m	1009 m		+172 m	+229 m	+161 m	+199 m
Juniperus communis	0.41	**0.50**	Area	10,349 km^2	14,222 km^2		−82%	−97%	−78%	−91%
			Elev.	1281 m	1372 m		+238 m	+407 m	+213 m	+308 m
Juniperus oxycedrus	0.42	**0.48**	Area	8077 km^2	13,339 km^2		+127%	+331%	+108%	+199%
			Elev.	1053 m	991 m		+61 m	+101 m	+53 m	+84 m
Juniperus thurifera	**0.48**	0.29	Area	9584 km^2	14,908 km^2		−53%	−53%	−52%	−53%
			Elev.	1157 m	1179 m		+26 m	+30 m	+29 m	+27 m
Pinus halepensis	0.30	**0.43**	Area	5340 km^2	5224 km^2		+124%	+368%	+79%	+302%
			Elev.	979 m	940 m		+24 m	+55 m	+16 m	+48 m
Pinus nigra ssp. *salzmannii*	0.41	**0.50**	Area	13,577 km^2	15,449 km^2		−44%	−55%	−42%	−48%
			Elev.	1183 m	1218 m		+26 m	+32 m	+25 m	+29 m
Pinus pinaster	**0.40**	0.23	Area	8595 km^2	12,180 km^2		+61%	+77%	+55%	+75%
			Elev.	1074 m	1059 m		+43 m	+93 m	+35 m	+63 m
Pinus sylvestris	**0.66**	0.47	Area	11,598 km^2	16,784 km^2		−87%	−98%	−84%	−93%
			Elev.	1377 m	1336 m		+261 m	+352 m	+237 m	+295 m
Quercus faginea	**0.41**	0.12	Area	11,436 km^2	18,436 km^2		−12%	−44%	−5%	−27%
			Elev.	1089 m	1103 m		+110 m	+157 m	+101 m	+131 m
Quercus ilex ssp. *ballota*	**0.41**	0.32	Area	23,612 km^2	33,020 km^2		+62%	+104%	+51%	+86%
			Elev.	1060 m	1014 m		+28 m	+85 m	+19 m	+54 m
Quercus pyrenaica	**0.58**	0.41	Area	10,329 km^2	16,642 km^2		−54%	−70%	−50%	−58%
			Elev.	1182 m	1257 m		+85 m	+112 m	+76 m	+96 m

lowlands showing the largest projected changes in the areas of species distribution (Fig. 2).

Forest structure (community maps)

Figure 3 shows the first axis of the MCA ordination of the matrix for the data on presence/absence of species under current and future scenarios. The axis illustrates the main trend in the variation in the composition of the current tree communities over the study area (77.1% of inertia was absorbed by the first axis), and represents the degree of adaptability of species to a water deficit in summer conditions (Table 3). The cells on the right contain Eurosiberian species (Eurosiberian coniferous and broad-leaved species), which are intolerant of summer drought: *Fagus sylvatica*, *J. comunnis* and *P. sylvestris*. The cells on the left contain the Mediterranean species (xeric conifers and sclerophyllous evergreen species), which are tolerant of high temperatures and summer drought, such as *P. halepensis*, *J. oxycedrus*, *Q. ilex* ssp. *ballota* and *P. pinaster*.

Shifts in communities are predicted to occur as a result of an increase in the area where the climate is Mediterranean (Fig. 3) as follows.

1. Expansion of Mediterranean forests. The greatest changes will occur in mountainous areas at low and mid-elevations. Our models predict a sharp increase in the proportion of perennial sclerophyllous species (*P. halepensis*, *P. pinaster*, *J. oxycedrus*, *Q. ilex*) together with a decline in semi-deciduous or deciduous species with moderate requirements for water (*Q. pyrenaica*, *Q. faginea*, *Fraxinus angustifolia*), which are found currently in the flat piedmont and low-elevation mountainous areas. In contrast, the range of xerophyllous vegetation, which at present occupies marginal areas in warm, dry, sheltered piedmont enclaves, will increase considerably, and it is likely that these trees will become the dominant vegetation formation in these areas.

2. Displacement of Eurosiberian forests. The coniferous forests that grow in cold regions (*P. sylvestris* and *J. communis*) and the Eurosiberian broadleaf forests whose optimum conditions are cold and wet (*Fagus sylvatica*) will undergo a clear latitudinal displacement towards the north and a large reduction in range. In the central and northern ranges, these forests will be replaced by oak forests of *Q. pyrenaica* and *Q. faginea*, and they will disappear from the westernmost mountains. In the case of mixed pine forests of *P. sylvestris* and *P. nigra* ssp. *salzmannii*, the proportions of *P. nigra* and
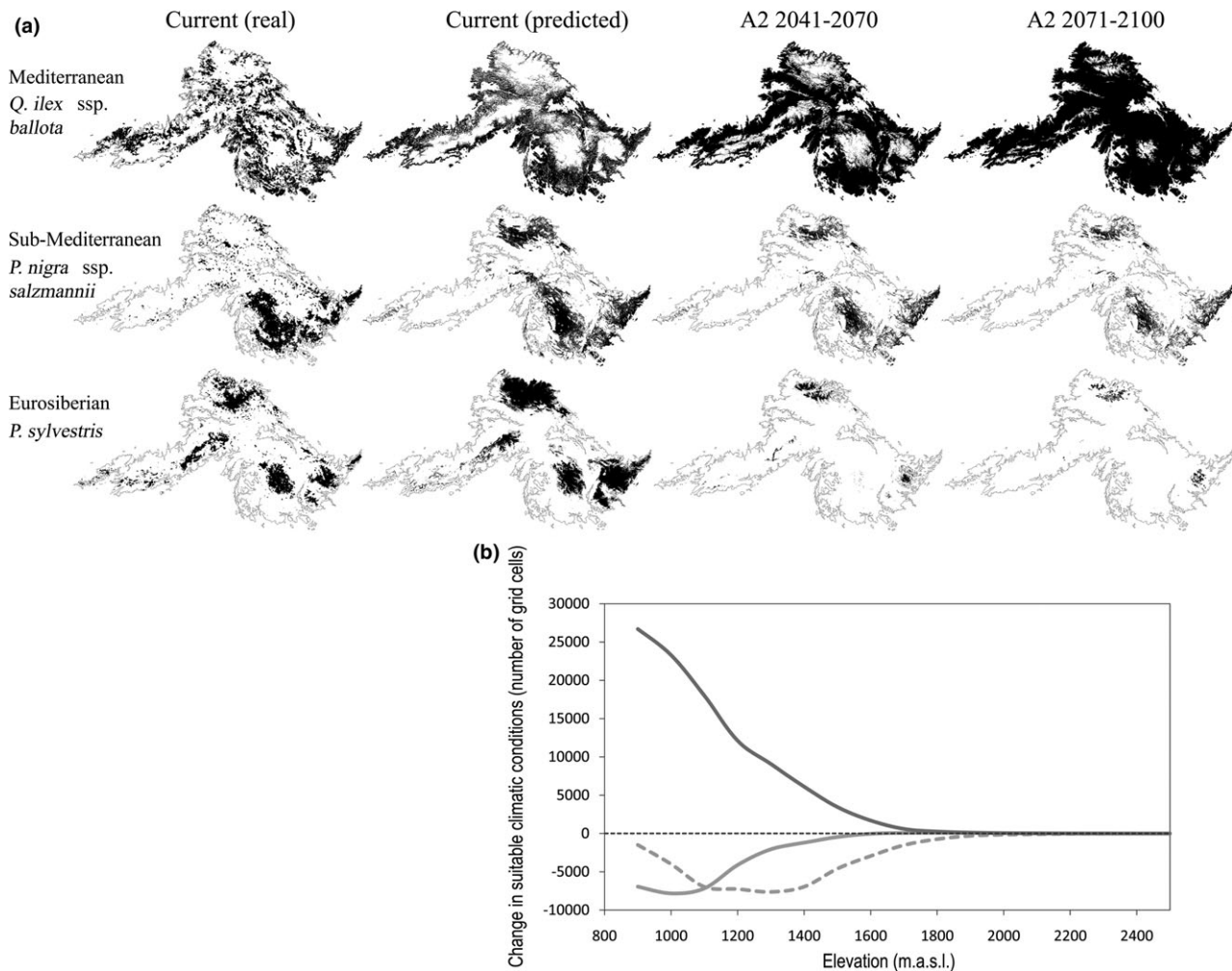
Figure 2 Current and projected distributions of tree communities in the Central and Iberian Mountain Ranges, under the A2 climate change scenario. (a) Three type species are shown from among the 15 species (Appendix S2): Mediterranean (*Quercus ilex* ssp. *ballota*), sub-Mediterranean (*Pinus nigra* ssp. *salzmannii*) and Eurosiberian (*Pinus sylvestris*). (b) Potential change in the distribution of all the species in each of these three groups. The curves represent the change in suitable conditions (number of grid cells) for these groups under the A2 2071–2100 climate change scenario in the ranges across the elevational gradient: Mediterranean species (dark grey line), sub-Mediterranean species (light grey), and Eurosiberian species (dashed grey).

*J. thurifera*, which are thermophilous species, are predicted to increase progressively.

DISCUSSION

The low resolution of both biological and abiotic datasets used in studies that assess the effects of climate change on mountain biodiversity has prevented the identification of small areas with environmental conditions that are suitable for particular species. This is a substantial limitation, because such micro-refugia might buffer the negative effects of climate change. Our study overcomes some of the limitations of previous studies. We used fine-scale abiotic and biotic data for both current and future conditions. These data included the distribution of trees in mountainous areas of Spain (high-resolution data from the Spanish Forestry Inventory) and key abiotic conditions that,

unfortunately, are usually overlooked in many studies that use SDMs, such as potential soil moisture (microtopographic issues were taken into account in the current study). Our results reinforce the widely accepted view that changes in mountain biota as a result of climate change will occur mainly at high elevations (Grabherr *et al.*, 1994; Beniston, 2000; Holten, 2001; Skov & Svenning, 2004). However, changes in the spatial extent of species ranges and in community composition will be greater at lower than at higher elevations. Therefore, changes in species distributions and forest communities are expected to occur across the entire range of elevation.

The projections of our models are consistent with previously observed trends reported by Zavala *et al.* (2000), Mooney *et al.* (2001) and Sobrino *et al.* (2001), among others. These reports suggest that thermophilous tree species on the Iberian
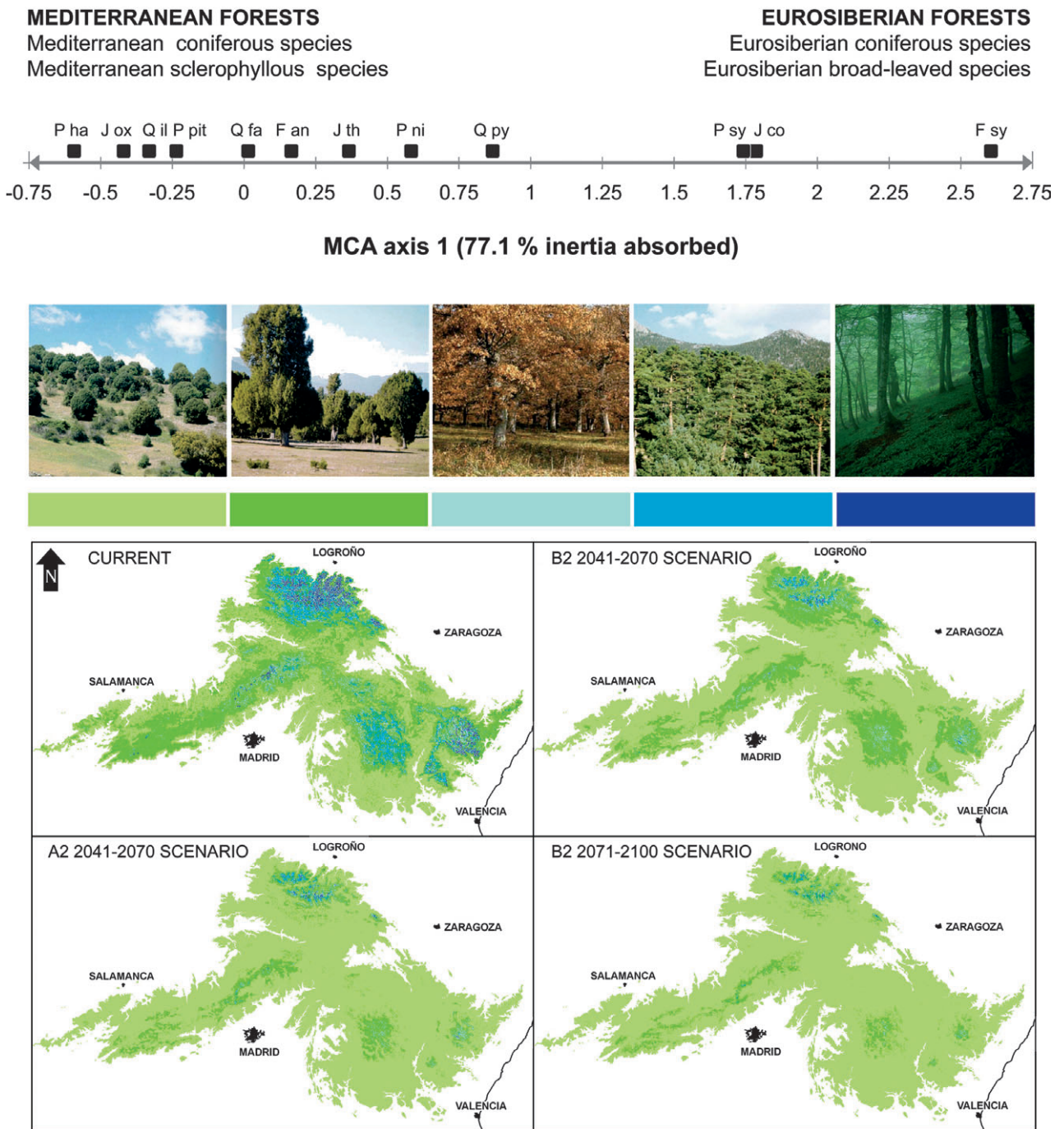
Figure 3 Changes in tree communities projected for the Central and Iberian Mountain Ranges in the Iberian Peninsula. At the top, the first axis of the multiple correspondence analysis (MCA) ordination of the data on presence/absence of species for current and future scenarios is shown with the coordinates of the 12 species modelled (Pha = *Pinus halepensis*, Jox = *Juniperus oxycedrus*, Qil = *Quercus ilex*, Ppit = *Pinus pinaster*, Qfa = *Quercus faginea*, Fan = *Fraxinus angustifolia*, Jth = *Juniperus thurifera*, Pni = *Pinus nigra*, Qpy = *Quercus pyrenaica*, Psy = *Pinus sylvestris*, Jco = *Juniperus communis*, Fsy = *Fagus sylvatica*). We identified current and future types of forest by segmenting the axis into five equal intervals on the basis of the coordinates of the cells represented on the axis. The forest structure in the current scenario, B2 scenario for 2041–70, A2 scenario for 2041–70, and B2 scenario for 2071–2100 is shown under the photographs. The forests vary from Mediterranean forests, which are very tolerant of summer water deficit (light green), to Eurosiberian forests, which are intolerant of summer water deficit (dark blue).

Peninsula will spread in response to climate change due to an increase in the duration of the vegetative period and a decrease in the availability of water. Thus, during the 21st century, the proportion of sclerophyllous species, which are resistant to high temperatures and to water deficit in summer, could increase, whereas the Eurosiberian species that are found in

Table 3 Contributions of the tree species to the first axis of the multiple correspondence analysis (MCA) (77.1% of absorbed variance). The coordinates of the abiotic variables (external variables) on the first ordination axis are shown at the bottom of the table.

Species	MCA axis 1 coordinate
Pinus halepensis	−0.593
Juniperus oxycedrus	−0.420
Quercus ilex ssp. *ballota*	−0.330
Pinus pinaster	−0.236
Quercus faginea	0.013
Fraxinus angustifolia	0.166
Juniperus thurifera	0.365
Pinus nigra ssp. *salzmannii*	0.586
Quercus pyrenaica	0.869
Pinus sylvestris	1.729
Juniperus communis	1.782
Fagus sylvatica	2.599
Mean annual temperature	−1.161
Mean daily maximum temperature (summer)	−1.145
Mean daily minimum temperature (winter)	−0.981
Annual thermal oscillation	−0.616
Sands and gravels (Tertiary)	−0.386
Sands and gravels (Quaternary)	−0.243
Granitoids (Hercynian)	−0.064
Hydric convergence index	−0.061
Limestone rocks (Mesozoic)	0.275
Gneisses (pre-Hercynian)	0.303
Autumn rain	0.311
Winter rain	0.314
Slates and quartzites (Palaeozoic)	0.325
Autumn, winter and spring rain	0.373
Annual rain	0.453
Spring rain	0.546
Summer rain	0.929

these mountains (i.e. cold-temperate and boreal species) could decline. Therefore, potential biotic attrition (Colwell *et al.*, 2008), *sensu* a decrease in species diversity, would occur in the lowlands of Mediterranean mountains under climate change. Species that are adapted to warm and dry conditions and currently occur at lower elevations of Mediterranean mountains would undergo an increase in range and become more dominant across these mountain ranges. The vegetation of lower regions could become much more xeric as a result of stress that would be induced by a lack of water. Such conditions currently affect some Mediterranean forests, in which the rate of evapotranspiration is equal to that of rainfall (Peñuelas, 2001). As a result of this process of aridification, our models predicted a sharp decrease in the geographical ranges of species such as *Q. pyrenaica* and *Fraxinus angustifolia*, together with the spread of xerophyllous vegetation (*Q. ilex* ssp. *ballota*, *J. oxycedrus*, *P. halepensis, P. pinaster*), which currently occupies warm and dry sheltered enclaves. A decline in range might already have begun in the oak forests of *Q. pyrenaica* in the centre of the Iberian Peninsula, and it is

likely that these forests will experience a sharp reduction in range as a result of the increased duration and recurrence of droughts that are predicted (Hernández-Santana *et al.*, 2008).

With regard to the broadleaf forests whose optimal conditions are cold and wet, the results predict a clear decrease in their range within our study area under all the scenarios of climate change. It is likely that these broadleaf forests, which are the most southerly examples of this type of forest in Eurasia, will suffer severe reductions in range in the mountains in the centre and north of the Iberian Peninsula, and they might disappear from isolated southern enclaves. The progressive substitution of cold-temperate species (*Fagus sylvatica*) by species with lower requirements for water, such as *Q. pyrenaica* in the southern ranges and *P. sylvestris* in the northern ones, is projected to occur during the 21st century. This pattern of replacement is consistent with the changes in areas of species distribution predicted by Gritti *et al.* (2006) for the Mediterranean Basin and with actual changes observed recently in Spain by Peñuelas & Boada (2003), Jump *et al.* (2006) and Benito *et al.* (2008).

Relict Mediterranean populations of Scots pine (*P. sylvestris*) have had a refuge in these mountains since the end of the last glaciation and constitute one of the southernmost formations of this species in Eurasia. The natural regeneration of this species at its lower-latitude limit might be seriously affected by the predicted increase in summer drought, which might provoke a decrease in recruitment (Escudero *et al.*, 1997; Martínez-Vilalta & Piñol, 2002; Castro *et al.*, 2004). Water deficit has also been recognized previously as a driver of recruitment levels, population performance and geographical range for other species in Mediterranean mountains, such as *Pinus uncinata* (Camarero & Gutiérrez, 2007), *Taxus baccata* (Sanz *et al.*, 2009) and *Abies pinsapo* (Linares & Carreira, 2009). Our projections, in accordance with those obtained by Benito *et al.* (2006, 2008) and Keenan *et al.* (2011), corroborate this pattern of desiccation, which would cause a clear northward displacement of *P. sylvestris* within our study area, together with a substantial reduction in its range. Our results also show an elevational displacement of this species, which is projected to invade high mountain grasslands. It appears that this displacement is already a reality in these mountains. For example, high mountain grassland communities that are typical of the Cryoro-Mediterranean belt are being replaced by shrub patches from lower elevations (Sanz-Elorza *et al.*, 2003).

There is palynological evidence that shows that the mountain ranges in the centre of the Iberian Peninsula were colonized from the north-east to the south-west by broadleaf and Eurosiberian conifer species during the Atlantic (7500–4500 years ago) and sub-Atlantic (2700–1000 years ago) periods (Costa *et al.*, 1998; Cheddadi *et al.*, 2006). Our results indicate that, under the climate change scenarios considered, the predicted retreat of these cold–wet forests and the spread of the semi-arid Mediterranean forests will involve exactly the opposite process; namely, the displacement of cold–wet forests towards the north-east and the spread of Mediterranean

vegetation from the piedmonts. This highlights the importance of the study of past population dynamics in improving our understanding of the future effects of climate change on biodiversity (Willis *et al.*, 2007) and promoting the adoption of proactive conservation strategies to aid the migration of species across their historical migration routes.

The changes predicted in this study might be delayed if the high concentrations of atmospheric CO_2 were to compensate to some extent for the effects of drought on the Mediterranean vegetation, a hypothesis that to date has provoked much debate (Osborne *et al.*, 2000; Martínez-Vilalta *et al.*, 2002). Alternatively, the changes might occur more rapidly than predicted if climate change were to accelerate over the next 50–100 years (Peñuelas *et al.*, 2009). Furthermore, the forests studied herein, which are located in an environment that is becoming increasingly fragmented, would face new disruptive factors, such as the spread of exotic thermophilous or xerophyllous species (Brasier, 1996; Gritti *et al.*, 2006), increasingly frequent natural and human-made fires (Moriondo *et al.*, 2006) and a higher incidence of insect pests that until now have only been observed at lower elevations (Hódar *et al.*, 2003). Therefore, it is necessary to determine the synergistic effect of all these disruptive factors in species distribution models (Pearson, 2006).

Although climate has been considered to be the main driver of the most important vegetation patterns (Körner & Paulsen, 2004), it should be noted that other processes not accounted for in our study, such as recruitment dynamics, may control the precise location of individual trees (Batllori *et al.*, 2009, 2010) at local scales. Future research should focus on the development of more mechanistic models that include population dynamics and inter-specific competition at a local scale to refine trends projected by SDMs (Nogués-Bravo, 2009; Keenan *et al.*, 2011).

CONCLUSIONS

The effects of climate change on mountain forests are projected to differ greatly between northern and southern Europe. At high latitudes, plant growth is limited fundamentally by temperature. Boreal and subalpine species, which are found at high and mid-elevations, are threatened the most by global warming (Grabherr *et al.*, 1994; Beniston, 2000; Holten, 2001; Skov & Svenning, 2004). Our results indicate that, in the mountains of southern Europe, the communities that will undergo the greatest changes in terms of their geographical ranges will be those found currently in the piedmont and at lower elevations in mountainous regions, although changes will also occur at high elevations. The projected changes in range will result from an increasing water deficit. It is likely that aridification will reduce the geographical ranges of broadleaf forests, and that Eurosiberian conifers at mid- and high elevations will be displaced by Mediterranean sclerophyllous species. Given that in mountain ranges the area of land at low or mid-elevations is usually greater than that at high elevations (Körner, 2007), changes in the spatial extent of

mountainous forest communities will probably be greater at low elevations.

Our results from models with high spatial resolution confirm the exposure of cold-adapted tree species to dramatic changes in range under global warming, as was reported by previous studies that used models with a lower resolution (Thuiller *et al.*, 2005). However, the following considerations should be taken into account to prevent oversimplification of our findings. First, the ranges of species in Mediterranean mountains have expanded and contracted before, during the Quaternary (Carrión, 2002; González-Sampériz *et al.*, 2006; Fletcher & Sánchez-Goñi, 2008; Rubiales *et al.*, 2008; Cheddadi *et al.*, 2009), and such changes may well be considered part of the natural dynamic of forest ranges in Mediterranean mountains. However, it is worth noting that current landscapes in Mediterranean mountains are highly fragmented and that, as a result, such dynamics might be disrupted significantly in the near future. Second, new approaches that use biological and abiotic data for mountain environments at even higher resolution have confirmed that the high density of microrefugia in mountains may buffer the effects of climate change on biodiversity (Scherrer & Körner, 2011).

Populations of temperate forests that are located at their lower-latitude limit have critical importance as long-term resources to maintain the genetic diversity of species, as foci of speciation and as key elements that provide ecosystem services. Our study highlights the fact that Mediterranean mountains might lose their role as refugia for cold-adapted species and hence a significant part of their genetic heritage. Given that climate change has the potential to drive species out of current reserves (Araújo *et al.*, 2004, 2011), there is a need for realistic conservation measures that consider climate change (Hampe & Petit, 2005; Körner *et al.*, 2007).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Location of the meteorological stations in the study area, the datasets from which we used to map current and future climatic conditions: (a) rainfall stations (752 stations); (b) temperature stations (197 stations).

Appendix S2 Current and potential distributions of species simulated for the ECHAM4 scenarios considered.

Appendix S3 Abiotic variables included in the generalized linear models (GLMs) and data mining models (gradient boosting).

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BIOSKETCHES

Diego Ruiz-Labourdette is studying 'biocenosis–climate relationships' in Mediterranean ecosystems as the subject of his doctoral thesis. This article has been developed in the Landscape Ecology Group, Department of Ecology, Complutense University of Madrid, which collaborates with other universities, scientific research councils (CSIC), and non-governmental organizations, mainly the World Wildlife Fund (WWF), on numerical models, nature conservation and relationships between socioeconomy and landscape.

Author contributions: D.R.L., D.N.B., M.F.S. and F.D.P. designed the research and wrote the manuscript. D.R.L., D.N.B. and H.S.H. worked on the species distribution models, discussed analyses and interpreted the results. M.F.S. designed the multivariate analysis of the presence/absence data matrix and its interpretation and presentation. All authors have seen and approved the final manuscript.

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