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Potential impacts of climate change on habitat suitability of *Fagus sylvatica* L. forests in spain

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ABSTRACT

Fagus sylvatica forests are considered to be of Community interest according to Directive 92/43/EEC. Climate change predictions for Spain point to a warming scenario, coupled with decreasing rainfall, which may have an impact on their future distribution particularly at the extremes of its distribution area. Species distribution models incorporating bioclimatic, topographic and phytogeographic variables were used as predictors to assess their habitat suitability under current conditions and a climate change projection. Ten single models were generated and an ensemble-forecasting model was subsequently built by computing a consensus of single-model projections. The results revealed that ombrothermic indices are the main factors controlling the distribution of Spanish beech forests. They are highly vulnerable to climate change and could suffer a decline in their habitat suitability if climate trends observed are maintained in the future. The least favoured areas for them will be located close to the limit between the Temperate and Mediterranean climates, where they could suffer a loss of habitat suitability. Conversely, suitable new areas could be found mainly in western areas of the Cantabrian Range and in the Central Pyrenees.

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Bioclimatology; climate change; *Fagus sylvatica*; habitat suitability; MaxEnt; Phytogeography; Spain

Introduction

Climate is considered one of the most important environmental factors controlling the distribution of species and vegetation (Woodward 1987; Rivas-Martínez et al. 2011).

According to the Fifth Assessment Report (AR5) (IPCC 2014), the climate system is unequivocally warming, and many of the changes seen since the 1950s are unprecedented in either decades or millennia. The global average combined land and ocean surface temperature data calculated as a linear trend showed a warming of 0.85 [0.65–1.06] °C (confidence interval at 90%) in the period 1880–2012. The report also shows that average precipitation over the mid-latitude land areas in the Northern Hemisphere has increased since 1901 (medium confidence before and high confidence after 1951).

There is evidence that climate change is a significant driver of biodiversity loss (Millennium Ecosystem Assessment 2005), and yet predicting species' responses to climate change is a major challenge for ecology and biodiversity conservation (Rabasa et al. 2013). Changes in community structure, geographic distribution, dynamics and composition have been observed at ecosystem levels, while alterations in phenology, shifts in geographic distribution and physiological modifications have been reported at the species level (Guisan and Zimmermann 2000; Parmesan 2006; Ruiz-Labourdette et al. 2012). Spatial distribution models (SDMs) have become key in evaluating the impact of climate change on species and habitat distribution (Araújo et al. 2011; Rodríguez-Castañeda et al. 2012; Lötter and le Maitre 2014). In this context, Maximum Entropy models (MaxEnt) (Phillips et al. 2006) have become very popular for predicting the distributions of different species of flora and fauna and for forecasting future distributions under climate change (Lötter and le Maitre 2014).

The natural vegetation of a territory, among other factors, is a faithful reflection of its soil and climate conditions. The ecological science that studies the relationships between climate and the distribution of living organisms is known as Bioclimatology.

The Worldwide Bioclimatic Classification System (WBCS, Rivas-Martínez et al. 2011) has essentially focused on establishing a valid bioclimatic typology with an accurate relationship between climatic values (parameters and bioclimatic indices) and vegetational models for the whole Earth. In view of the high predictive value of bioclimatic units, bioclimatology can be used in programs for the study and conservation of biodiversity or habitats and in research into climate change and to determine future climate and vegetation scenarios (Rivas-Martínez et al. 2011).

Fagus sylvatica L. (European beech) is widely distributed across Europe and is one of the symbols of the European broadleaved forest with fundamental importance to European biodiversity, as it has a diverse array of dependent plants, animals and other organisms. The European Habitats Directive

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(Habitats Directive) (EEC 1992) highlights beech forests as a forest type of community importance. Article 17 of the Habitats Directive states that all Member States are required by the Directive to monitor habitat types and species considered to be of Community interest.

Fagus sylvatica is summer drought sensitive (Ellenberg 1988; Leuschner et al. 2001; Granier et al. 2007), and any possible adverse effects on its sustainability and regeneration may have a far-reaching ecological and economic impact (Fotelli et al. 2009). Climate change will mean that some beech forest habitats at the southern edge of their range are unlikely to be maintained in the future, whereas additional habitats may develop at their northern limit (Jump et al. 2006; Winkel et al. 2015).

The diversity of Spanish beech forests and their occurrence in both Eurosiberian and Mediterranean biogeographic Regions make Spain an ideal place to study potential changes in their habitat suitability caused by climate change. These forests have in Spain their southern and westernmost limit of distribution, so their maintenance and conservation is very important and necessary.

The main aims of this study were to identify the fundamental factors driving the distribution of Spanish beech forests and to model their habitat suitability under both current conditions and a future climate projection. To carry out this study, we used Species Distribution Models incorporating as newness the last approaches in Bioclimatology (Rivas-Martínez et al. 2011, 2017a) and Phytogeography (Rivas-Martínez et al. 2014, 2017b).

Material and methods

Study area

The study area comprises continental Spain, located in southwest Europe at 36°–44° N and between 10° W and 3° E, and with an area of 493,892 km^2 (Figure 1).

Its location and the complex orography lead to a high variability in the spatial distribution of temperature (Font 2000), making it particularly interesting from a climatic point of view. Its location and the complex orography lead to a high variability in the spatial distribution of temperature (Font 2000), making it particularly interesting from a climatic point of view. The average annual temperature decreases from south to north and from the coast inland (Capel 2000). The rainfall regime is characterized by high variability in both spatial and temporal terms and summer is the least rainy season.

Areas where beech forests can grow in Spain are characterized by mean annual temperatures ranging from (7° to 15 °C) and mean annual rainfall from 900 to 2500 mm (Sánchez de Dios et al. 2016).

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Figure 1. Study area. Source: Authors.

Forestry data

Fagus sylvatica forests in Spain are essentially distributed in the western Pyrenees and the central and eastern parts of the Cantabrian Range and the Basque mountains. They have a more sporadic presence in the more southerly mountainous areas including the Pre-Pyrenees, the Iberian and Central Range, and the Catalan coastal range (Rodríguez-Guitián et al. 2003; Olano and Peralta de Andrés 2008, 2009a, 2009b). These forests lie on the south-west boundary of their European distribution, making them more vulnerable to changes in climate and management (Jump et al. 2006; Aitken et al. 2008).

These formations represent different types of plant communities, which are considered of interest for conservation and are legally protected under the European Habitats Directive (EU Directive 92/43/EEC; Annexe I). Spanish beech forests refer to the following habitats in the Directive: 9110: *Luzulo-Fagetum* beech forests, 9120: Atlantic acidophilous beech forests with *Ilex* and sometimes *Taxus* in the shrub layer (*Quercenion robori-petraeae* or *Ilici-Fagenion*), 9150: Medio-European limestone beech forests of the *Cephalanthero-Fagion* and 9180*: *Tilio-Acerion* forests of slopes, screes and ravines.

The georeferenced distribution data for these habitats were obtained from the Spanish Inventory and map of the Directive 92/43/EEC habitat and from the Forest Map of Spain 1.50000 (MFE50). The maps were rasterized using analytical tools to a 700 × 700 m grid format for modelling purposes and converted into points, which were located in the centre of all the cells using ArcGis 10.2 conversion tools for application in a species distribution model.

Predictor variables

Current conditions

Climate variables (monthly temperature and rainfall data) were derived from the Digital Climate Atlas of the Iberian Peninsula (Ninyerola et al. 2000). The bioclimatic layers at a spatial resolution of 700 m (~0.5 km^2) were generated from these data using Map Algebra.

We initially took into account the parameters and bioclimatic indices used to characterize plant communities proposed by Rivas-Martínez et al. (2011) to generate the bioclimatic layers such as:

Tp (positive annual temperature), **Pp** (positive annual precipitation), **Ic** (continentality index), **Io** (annual ombrothermic index), **Ios** (summer ombrothermic indices), **It/Itc** (compensated thermicity index) (Database S1).

The Rivas-Martínez's model refers to the main climates, biomes and biogeographic units recognized on Earth. The knowledge of the distribution of vegetation (studied by Biogeography) makes possible to recognize bioclimatic and vegetational frontiers with higher accuracy. A biogeographic layer to district level according to Rivas-Martínez et al. (2014, 2017a, 2017b) was used in the current study. Additional layers such as model digital terrain (MDT), aspect and slope were also taken into account in this study.

To avoid multicollinearity problems we performed a pairwise correlation using the Spearman's rank correlation coefficient. We retained only predictors that showed a high relative contribution to the models and were not highly correlated ($r \leq |0.7|$). The final set of predictors representing the current conditions included nine variables: five bioclimatic layers (Io, Ios_2, Ios_3, Ic, Tp), three topographic variables (elevation aspect, slope) and biogeography.

Climate change scenario

A future climate projection was used to simulate changes in habitat suitability for Spanish beech forests under climate conditions for the 2050 period. This projection was generated based on the monthly, seasonal and annual rainfall and temperature trends observed in previous studies over the last five decades in Spain (del Río, Herrero, Fraile, et al. 2011; del Río, Herrero, Pinto-Gomes, et al. 2011; Ríos-Cornejo 2015).

The trends observed were applied to the current rainfall and temperature values to generate the future bioclimatic layers for the 2050 horizon (Io, Ios_2, Ios_3, Ic, Tp), using geostatistical analysis tools and Map Algebra with ArcGis 10.2.

Input data for altitude, slope, aspect and biogeography variables were considered as remaining constant in the 2050 scenario. Future habitat suitability for beech forests was also projected on the assumption that current vegetation–climate relationships will remain unaltered in a climate change situation.

Distribution modelling

The Maximum Entropy Modelling algorithm (MaxEnt) included in Biomod version 2 (Thuiller 2003) in R-CRAN 3.2.1 (R Development Core Team 2015) was used to model the habitat suitability of *Fagus sylvatica* forests under both current climate conditions and in a climate change projection for the 2050 horizon.

To evaluate the quality of the predictions, the occurrence data were randomly partitioned into 80% for training and 20% for testing (Fielding and Bell 1997). We used the recommended default parameters for MaxEnt (Phillips and Dudík 2008) and for Biomod (Thuiller et al. 2009). The procedure was replicated ten times to obtain more robust estimates (Elith et al. 2011).

Two different statistical measures available in Biomod were considered to estimate model performance: Area Under the Curve (AUC) of a Receiver Operating Characteristic plot (ROC) and the True Skill Statistic (TSS). We also use TSS to obtain information on the specificity and sensitivity of the generated models. Specificity reflects a model's ability to correctly predict an absence at a location, and sensitivity reflects a model's ability to correctly predict a presence at a location (Freeman and Moisen 2008).

An ensemble-forecasting model by computing a consensus of single-model projections (Araújo and New 2007; Thuiller et al. 2009) was later generated. The ensemble model was built giving higher importance to models with a better performance according to the AUC and TSS criteria (only models with AUC ≥ 0.9 and TSS ≥ 0.8 were selected to create the ensemble model), and using the median probability of occurrence across the selected models for each grid cell.

A probability threshold that maximizes sensitivity and specificity was selected to transform the results of distribution modelling from probabilities to a binary map (of 0 and 1) and differentiate suitable and non-suitable areas for Spanish beech forests. This threshold proved to be a good approach for threshold determination (Allouche et al. 2006; Jiménez-Valverde and Lobo 2007). Maps of habitat suitability were imported into ArcGis 10.2.

Predictions in novel environments were assessed using Multivariate Environmental Similarity Surfaces (MESS) (Elith et al. 2010, 2011). It measures the similarity between the environments used to train the model and the new projected environments for any grid cell. Caution is required when interpreting the results when a non-analogue climate is detected (Fitzpatrick and Hargrove 2009).

Finally, we analyzed the losses, gains or maintenance of suitable areas in the 2050 horizon and the Vulnerability Index (VI) according to Felicísimo et al. (2012). This index can be used as an indicator to define priorities in conservation policies.

Table 1. Per cent contribution of variables to ten single models (runs).

	Run 1	Run 2	Run 3	Run 4	Run 5	Run 6	Run 7	Run 8	Run 9	Run 10
Biog	30.4	31.4	32.2	30.5	34.6	33.6	29.7	35.8	31	31.9
Ios_3	19.1	19.2	19.5	19.6	17.9	18.2	19	18.2	19.4	20.3
Tp	13.7	14.1	14.6	14.6	13.4	15.2	15.3	14.2	14.7	14.5
Io	9.7	8.1	8.2	8.8	11.8	7.4	9.7	10.3	9.2	8.5
Ios_2	7.9	7.5	7.7	7.3	6.9	6.9	6.6	5.8	7.1	6.7
Asp	6	6.1	5.2	5.5	4.9	5.9	6.5	5.2	6.3	5.6
Ic	5.8	6.4	6.5	6.7	4.9	5.6	6.2	5.7	6.6	6
Elev	3.9	5	3.4	3.6	4.1	3.7	4.3	3.2	2.9	3.5
Slope	3.6	2.2	2.6	3.2	1.5	3.4	2.7	1.5	2.8	3

Biog: biogeography; Asp: aspect; Elev: elevation.

Results and discussion

AUC values ranged from 0.97 to 0.98 for the ten single models, and TSS values were between 0.88 and 0.9 (Figure S1). This implies that our models had excellent predictive ability, and the distribution of Spanish beech forests is therefore well described by the selected predictors. Sensitivity percentages ranged from 96.34 to 98.71 (obtained from TSS) and from 97.18 to 98.27 (from ROC). Specificity values were between 91.20 and 92.15 (from TSS) and between 91.25 and 92.20 (from ROC) (Figure S2).

The bioclimatic variables with the highest contribution to single models were the ombrothermic indices (particularly Ios_3 and Io) and Tp (Table 1). The importance of ombrotermic indices for characterizing deciduous forests has been previously reported by del Río et al. (2005). Our results agree with the proposal of Ellenberg (1988), who states that the main limitation to the natural distribution of beech is the availability of water.

Biogeography was also a very important variable in our models (Table 1). The incorporation of this variable in species distribution models gave good results in some preceding research works (Alfaro et al. 2015).The incorporation of this variable in species

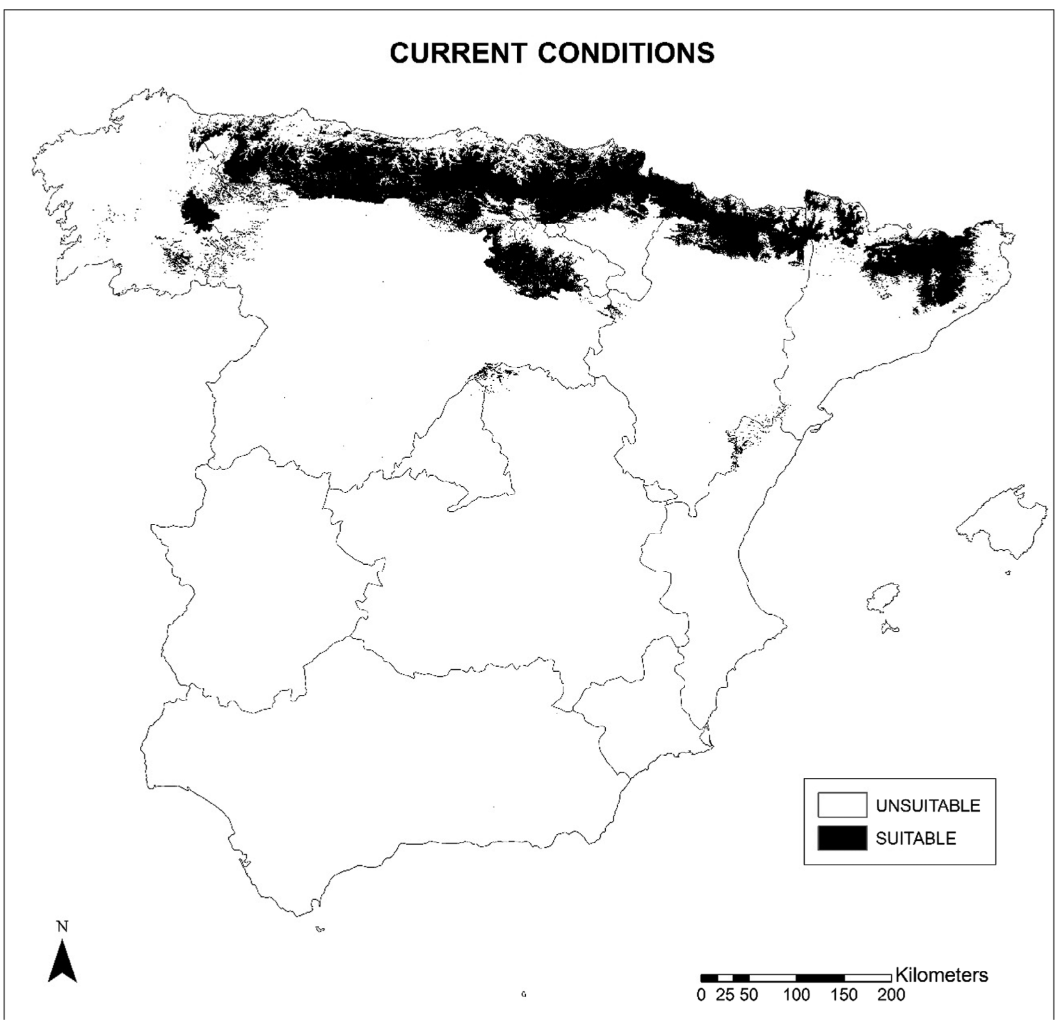

Figure 2. Habitat suitability for *Fagus sylvatica* forests in Spain under current conditions. Source: Authors.

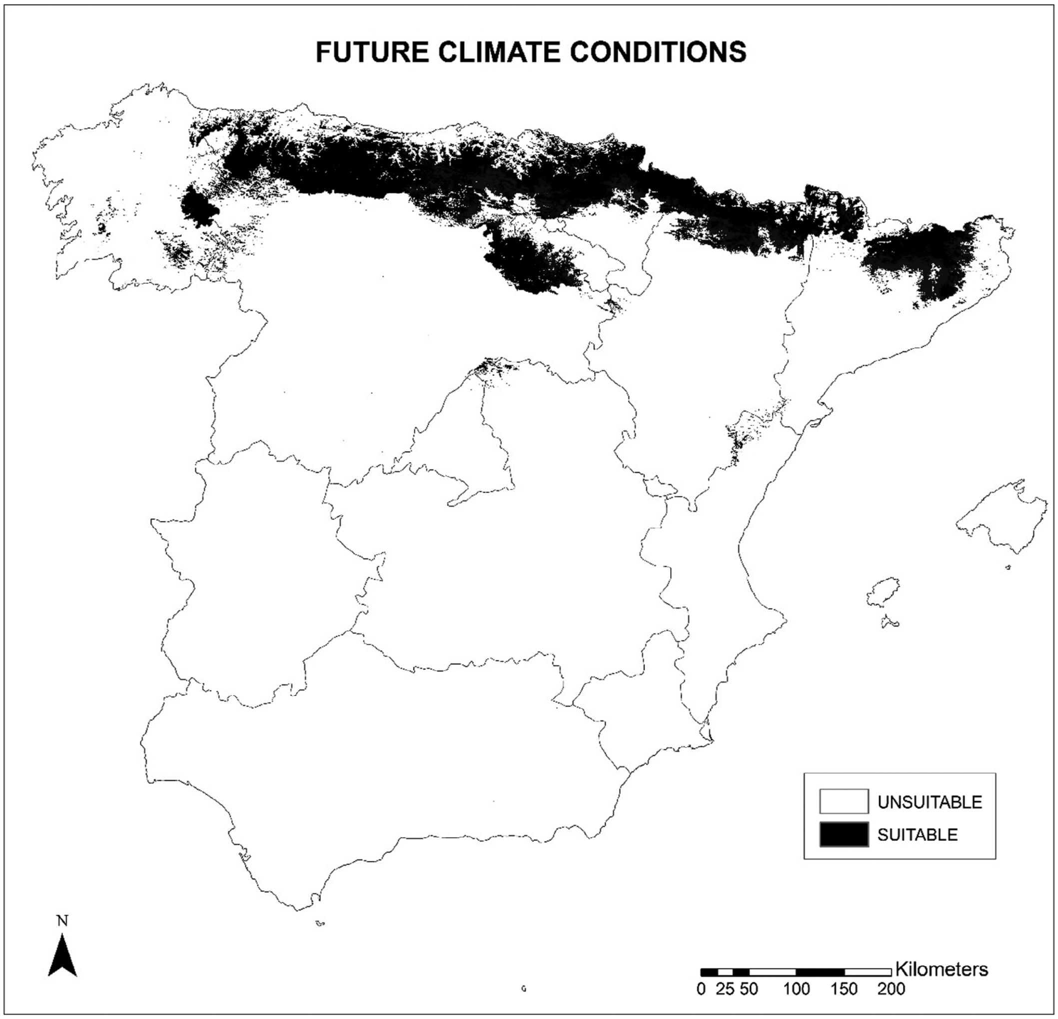

Figure 3. Habitat suitability for *Fagus sylvatica* forests in Spain under a climate change scenario (2050 period). Source: Authors.

distribution models gave good results in some preceding research works (Alfaro et al. 2015).

All ten previously developed single models were considered for the final ensemble forecasting. The TSS value was 0.89, and sensitivity and specificity values were 98.39 and 91.85, respectively.

Figure 2 shows the suitable areas for Spanish beech forests under current conditions occupying an extension of 46,861.15 km^2. The data are similar to those reported by Felicísimo et al. (2011), although they studied *Fagus sylvatica* as a species rather than as a forest, as in the present study. These areas are located in the Pyrenees, Cantabrian Range, Basque mountains and the Iberian System, and have a good match with the known distribution of this type of vegetation and with the potential vegetation map of Rivas-Martínez (1987). They mostly belong to the Orocantabrian, Cantabrian-Atlantic and Central Pyrenean biogeographic subprovinces, and to northern areas of the East Pyrenean and Oroiberian subprovinces. The southernmost beech forests are found in two small areas in the Central System and in Beceite Pass, all of which have a Temperate macrobioclimate (without, or with attenuated, summer drought) (submediterranean bioclimatic variant).

Temperature and rainfall trends reported for Spain during the last decades (del Río, Herrero, Fraile, et al. 2011; del Río, Herrero, Pinto-Gomes, et al. 2011; Ríos-Cornejo 2015) showed a general increase in temperature and decrease in rainfall what will also imply changes in tendencies of bioclimatic indices. A generalized trend to go down is observed in the ombrothermic indices (basically Ios_3 and Io) (Figure S3). Summer ombrothermic indices are very useful to discriminate the frontier between Mediterranean and Temperate macroclimates and also to establish the submediterranean bioclimatic variant (Rivas-Martínez et al. 2011) in areas with Temperate macrobioclimate.

The results of this research reveal that Temperate macrobioclimate might reduce its extension in future, mostly in the southernmost limits of its central and eastern territories (Pyrenean province and Oroiberian subprovince), due to decreases in their ombrothermic indices. Nevertheless, it is worth mentioning that western areas of the country (some of them belonging to the Orocantabric and Cantabro-Atlantic subprovinces, where beech forests grow) reveal higher values of these indices in 2050 than nowadays (Figure S3). This fact is fundamental to understand possible changes in the suitability areas of these forests as we will later comment.

The results of this research reveal that areas with a Temperate macrobioclimate may be reduced in future, mostly in the southernmost territories of the central and eastern areas, due to decreases in their ombrothermic indices.

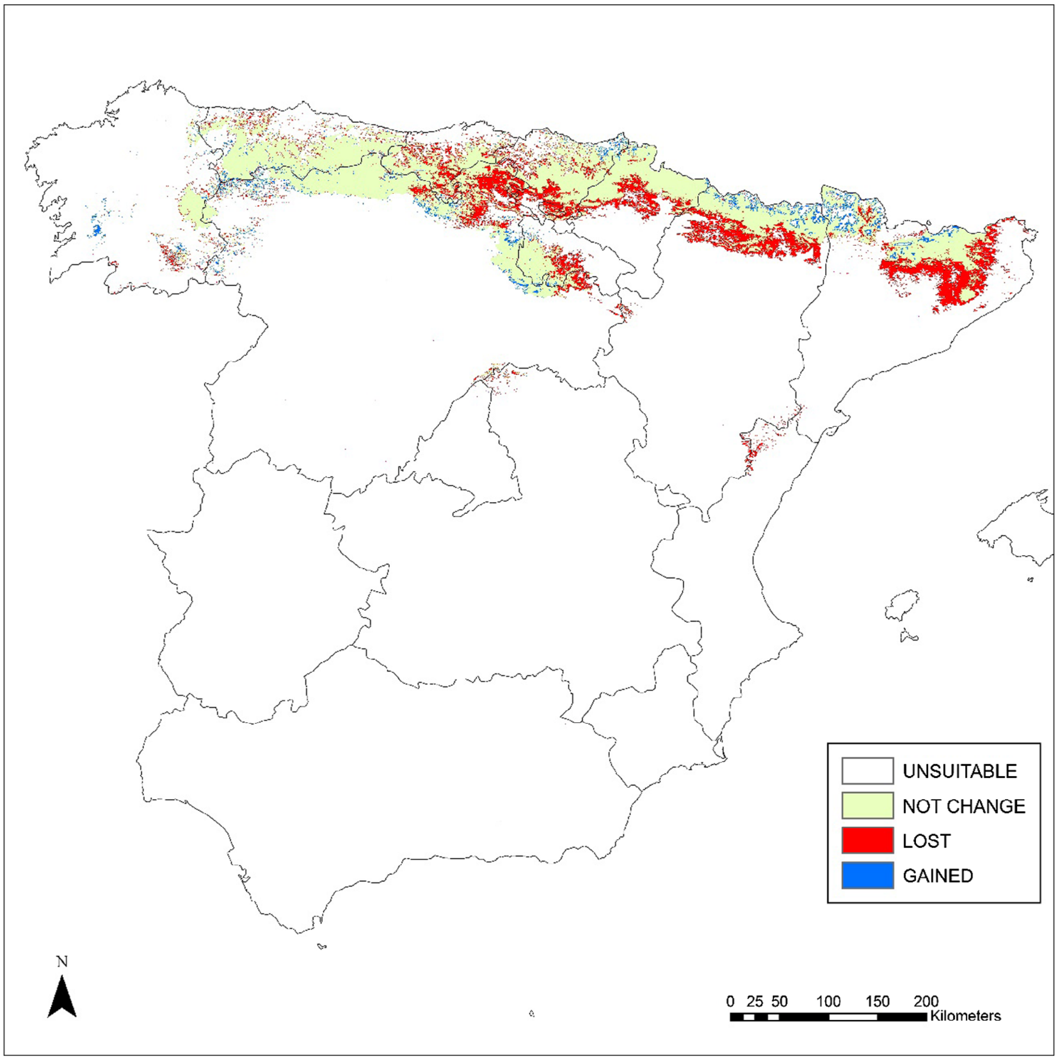

Figure 4. Loss, maintenance and gain in suitable areas for *Fagus sylvatica* forests for the 2050 period. Source: Authors.

Table 2. Median and interquartile range (25th and 75th percentiles) for the variables studied (current and future).

	CURRENT		2050	
	Median	25th–75th	Median	25th–75th
Altitude	950	694–1253	1058	789–1387
Io	8.8	6.8–11.3	8.6	6.6–10.9
Ios_2	2.9	2.2–3.8	3.2	2.6–3.9
Ios_3	3.5	2.8–4.1	3.3	2.7–4.1
Ic	15.4	14.1–16.8	15.3	14.1–17.0
Tp	1212	1038–1350	1235	1036–1394
Aspect	180.9	76.1–276.1	179.8	70.7–282.1
Slope	12.3	6.7–18.6	14.2	6.6–10.9

Figure 3 shows the habitat suitability for *Fagus sylvatica* forests in 2050, covering an area of 35,681.31 km^2 (46,861.15 km^2 in current situation). Figure 4 shows the predicted change in suitability in future, with the loss, maintenance and gain of suitable areas for the forests studied. Unchanged areas are seen to be predominant, as the suitable habitat will be maintained at 33,159.28 km^2 (70.76%). New areas with a suitable habitat (2522.03 km^2) (5.38%) are forecast to occur mostly in the western territories of the Orocantabrian subprovince, in the Cantabrian-Atlantic subprovince and in northern areas of Central Pyrenean and East Pyrenean subprovinces. The increase in potential habitat in Orocantabric and Cantabro-Atlanic subprovinces may be related to the rise in the ombrothermic indices previously mentioned for the 2050 period. Sánchez de Dios et al. (2016) also reported that population of *F. sylvatica* in NW Spain is expanding. Those authors and Muñoz-Sobrino et al. (2009) suggest that factors other than climate seem to be related to that expansion (land use abandonment and vegetation disequilibrium at the leading edge caused by post-glacial migration lags).

The trend to Tp increase and Io decrease could be associated with the presence of *F. sylvatica* forests at more northern latitudes and higher altitudes than nowadays. This expansion towards the north of the cold-temperate forests has been also proposed by Ruiz-Labourdette et al. (2012). Although more parameters than climate should be taken into account (competition among others) beech forests might replace or co-exist with forests of *Abies alba* Mill., *Pinus sylvestris* L. var. *pyrenaica* Svoboda and *Pinus sylvestris* L. var. *catalaunica* Gaussen) in Pyrenees because these forests are less tolerant to heat than beech (Meier et al. 2011).

The potential suitable areas for Spanish beech forests in 2050 could be decreased by 11,179.84 km^2 (23.86%). The territories with losses in habitat suitability are mostly located in southern areas close to the frontier with the Mediterranean macrobioclimate (with summer dryness) in the Oroiberian subprovince and in eastern areas (Pre-Pyrenean and East Pyrenean subprovinces). The increase of areas with Mediterranean and submediterranean climates may be related to this loss of suitable habitat. Jump et al. (2006) reported a rapid decline in beech forests in northeastern Spain due to intense warming and drought. The most sensitive habitat to the reduction in suitability is 9150 (Medio-European limestone beech forests of the *Cephalanthero-Fagion*), as these forests grow in temperate areas with a very important influence of the Mediterranean climate (under the submediterranean bioclimatic variant). The European Red List of Habitats (2017) also points out a decreasing trend in quantity of these forests for Spain.

Finally, the current southernmost beech forests (in the Central Range and the relict forests in the Beceite Pass) may disappear by 2050.

Figure S4 shows the Multivariate Environmental Similarity Surface (MESS map) including areas where predictions in 2050 could be uncertain (in black). A comparison of this map with the habitat suitability for 2050 showed that our predictions could be less accuracy in some new areas in the north of Spain (Basque Country and Navarre). Negative MESS values mean that at least one variable has a value outside the range of the reference set, and positive values indicate that the variables are within the bounds of the reference set.

Table 2 shows the median and 25th and 75th percentiles for the predictor variables in the study (current and future). The middle ranges of Io and Ios_3 may be lower in future due to rising temperatures and decreasing rainfall, which may imply changes in the distribution of beech forests in the southernmost areas close to the Mediterranean macrobioclimate. As mentioned previously, the increase in the median and inter-quartile range of Ios_2 could potentially favour the extension of beech forests in the western areas of the country. The trend towards climate warming may lead to a slight increase in the positive temperature range while continentality will remain unchanged. Our predictions also highlight a general upward shift (100 metres approximately) in the altitudinal distribution of this forest, agreeing with the findings of Peñuelas and Boada (2003) and Jump et al. (2006). Kramer et al. (2010) also reported a northward shift in the southern distribution limit of *Fagus sylvatica* and a northward extension of the northern limit.

The result for the Vulnerability Index (VI) for these forests was 0.92 (B category) ($0.85 \leq VI < 0.95$), indicating very high vulnerability. This result agrees with the findings of Felicísimo et al. (2012) for the species *Fagus sylvatica* for the period 2041–2070 (CGM2/B2).

To conclude, it should be noted that our models represent only habitat suitability. We are aware of the limitations and uncertainties of SDMs as mentioned by other authors, as they may overlook aspects such as competition, adaptive responses, vegetation disequilibrium at the leading edge caused by post-glacial migration lags, human activities and other local processes (Rouget et al. 2001; Araújo and Luoto 2007; Sánchez de Dios et al. 2016). Nevertheless, they continue to be a very useful tool for assessing potential species ranges under current or changed conditions (Pearson and Dawson 2003), and provide valuable information for policymakers and planners to adapt and conserve these forests in response to climate change.

Conclusions

An ensemble-forecasting model created by computing a consensus of ten single-model projections has been used in this study to model the habitat suitability of Spanish *Fagus sylvatica* forests under both current conditions and in a climate change projection for the 2050 horizon, using bioclimatic, topographic and biogeographic variables.

The present study highlights the high vulnerability of these forests and the decline in their habitat suitability if current climate trends are sustained in the future. The least favoured areas in 2050 will be located at the limit between the Temperate and Mediterranean macrobioclimates. New suitable areas are forecast to occur in western territories and in some areas of the Pyrenees. In agreement with other authors, our study reveals a general upward shift (100 m approximately) in the altitudinal distribution of this forest.

The authors suggest that the approach used in this study incorporating new advances in Bioclimatology and Phytogeography can be useful for its consideration in conservation and management policies of these forests that could be affected by climate change. Forest policy must take climate change risks into consideration to ensure effective mitigation and help conserve and maintain the benefits of these forests for society.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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