Original Articles

Modelling the impacts of climate change on habitat suitability and vulnerability in deciduous forests in Spain

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ABSTRACT

Global change is expected to impact on the distribution and abundance of forests. Spain represents the south-western limit of distribution for several types of deciduous forests and, as part of the Mediterranean Basin, it has all the characteristics to be affected by climate change. This study analyses the effects of climate change on habitat suitability and vulnerability in four categories of deciduous forests: *Fagus sylvatica* L., *Quercus petraea* (Matt.) Leibl., *Quercus robur* L. and *Betula celtiberica* Rothm. and Vasc. The approach combines an ensemble platform for species distribution models (SDMs) using three algorithms applied to four global circulation models (GCMs) driven by two representative concentration pathways (RCPs). Bioclimatic, biogeographic, soil and topographic variables were taken into consideration as predictors to build 320 single distribution models. Ensemble-forecasting models were then produced for each forest category and RCPs by computing a consensus of single-model projections. The adapted proposal of the Intergovernmental Panel on Climate Change (IPCC) was also applied to deal with the uncertainty and notify the likelihood of the outcomes.

The results revealed generalized losses in habitat suitability compared to current conditions for all the forest categories, which were more drastic for the RCP 8.5 emission pathway. Exceptions worth noting are forests of *Fagus sylvatica* (likelihood 25%-50%) and *Quercus robur* (likelihood 75%-100%) in the Orocantabrian biogeographic subprovince, and *Quercus petraea* formations in the Cantabrian Atlantic subprovince (likelihood 25%-50%). *Betula celtiberica* would suffer the largest losses of habitat suitability under the climate change scenarios analysed. The vulnerability analysis confirmed that the deciduous formations least affected by climate change in future will be the Orocantabrian forests, while the Pyrenean and Oroiberian communities are the most vulnerable.

The models developed in this study provide decision-makers with basic information and a useful tool for designing plans for the conservation and management of these forests in order to mitigate the impact of climate change. The study also highlights the importance and usefulness of conducting analyses at the biogeographic level, since the effects of climate change may be different and require management and conservation policies at local level.

1. Introduction

Climate is one of the most significant environmental factors influencing biodiversity and the distribution of vegetation (Woodward and Williams, 1987; Araújo and Pearson, 2005; Rivas-Martínez et al., 2011a; Williams et al., 2013; Guisan et al., 2013). The climate system is unequivocally warming, and many of the shifts observed since the 1950s are unprecedented over decades or centuries (Fifth Assessment Report,

AR5) (IPCC, 2014). The global average of the combined ocean surface and land temperature data calculated as a linear trend showed a warming of 0.85 [0.65 to 1.06] °C (confidence interval of 90%) in the period between 1880 and 2012. The Intergovernmental Panel on Climate Change (IPCC) also reveals that average precipitation has increased since 1901 (medium confidence before and high confidence after 1951) over mid-latitude land areas in the Northern Hemisphere. Values up to 40% has been observed in northern Europe but in contrast, the average precipitation in the southern parts of Europe has decreased by >20% (IPCC, 2001). One consequence of these changing conditions is that the Mediterranean Basin will experience lower rainfall and higher aridity (Klausmeyer and Shaw 2009; Vitale et al., 2012; López-Tirado and Hidalgo, 2018).

It is important to understand the ecological factors affecting the distribution of forests in order to plan appropriate management actions and prevent the potential impacts of climate change (Benito Garzón et al., 2008). Climate change will influence forest biodiversity on multiple levels and have direct and indirect impacts on forest ecosystems worldwide. Changes in phenology or physiological modifications have been reported at the species level, and in the dynamics and composition, community structure and geographic distribution at the ecosystem level (Guisan and Zimmermann, 2000; Parmesan, 2006; Bellard et al., 2012; Ruiz-Labourdette et al., 2012; Dunckel et al., 2017).

The most cost-efficient way to obtain information about potential shifts in the distribution of species and their communities is by modelling habitat suitability, which can predict the potential distribution of biota as a function of environmental factors (Casalegno et al., 2011). Species distribution models (SDMs) are currently the main tools for deriving spatially explicit predictions of environmental suitability for species (Jarvie and Svenning, 2018). They are used for species management, conservation biology, biogeography and climate change research. Nevertheless, SDMs inevitably include some degrees of uncertainty related to the inherent variability of natural systems (Gould et al., 2014; Porfirio et al., 2014; Taleshi et al. 2019; Noce et al., 2019). In this regard, ensemble forecasting has been revealed as an effective solution for quantifying the variation originating from a range of choices made during the modelling process and to reduce variability of SDMs. It is due the ensemble forecasting framework combines the outputs of several sources of uncertainty, and can improve the accuracy of climate change impacts (Buisson et al., 2010; Taleshi et al., 2019). Therefore, the approach allows more robust decision making in the face of uncertainty and having much to offer to conservation planning (Araújo and New, 2007; Zhang et al., 2015). This method can be also combined with General Circulation Models (GCMs) and emission scenarios to quantify uncertainties associated with model projections under climate change (Zhang et al. 2015; Vieilledent et al., 2013; Noce et al., 2017). Biogeography also plays a fundamental role when analysing relationships between forests and climate change (Bonan, 2008; Noce et al. 2019) and its incorporation together with bioclimatic variables in SDMs produced good results in several earlier investigations (Alfaro-Saiz et al., 2015; del Río et al., 2018).

The effects of climate change on deciduous forests have been studied from different points of view. Kramer et al. (2010), Morin et al. (2010), Vitasse et al. (2011), Xie et al. (2015), Estiarte and Peñuelas (2015), Dyderski et al. (2018), Seyednasrollah et al. (2020) and Liu et al. (2020) analysed the influence of climate change on the phenology of various deciduous tree species. Fibbi et al. (2019) studied the impacts of climate change on the gross primary production of Italian forests. Other researches investigated the future sustainability and survival of deciduous forests (basically of *Fagus sylvatica*): Peñuelas and Boada (2003), Jump et al. (2006), Thuiller et al. (2006), Benito Garzón et al. (2008), Lindner et al. (2010), Lindner et al. (2014), Stojanović et al. (2013), Ruiz-Labourdette et al. (2014), Roces-Díaz et al. (2014), del Río et al. (2018), Castaño-Santamaría et al. (2019), Fan et al. (2020).

However, to our knowledge no studies were conducted for the whole Spain using ensemble forecasting models with the inclusion of bioclimatic, biogeographic, topographic and soil predictors to model, at a low spatial resolution, suitable areas for deciduous forests under current conditions and future climate change scenarios.

The overall aims of this research are to identify the essential factors driving the distribution of Spanish deciduous forests, and to assess the impacts of climate change on the suitability and vulnerability of their habitat.

The novelties of this study are:

- The combination of the latest approaches in bioclimatology and biogeography with topographic and soil predictors.
- The use of an ensemble platform for SDMs combining three algorithms, four general circulation models (GCMs) and two different emission pathways.
- The addition of information on the likelihood of outcomes according to the IPCC terminology.
- The analyses are carried out at a low resolution and considering the biogeographic units where the forests occur.

2. Data and methods

2.1. Study area

The study was carried out in continental Spain, which extends from 36° to 44° N and 10° W to 3° E. It is the largest country in Southern Europe and covers an area of 493,892 km². Mainland Spain is a mountainous country, dominated by high plateaus and mountain chains. The major mountain systems are distributed from west to east. Starting from the north are the Pyrenees, which form a natural border with France; to the west of the Pyrenees and running parallel with the north coast is the Cantabrian Range; the Central System and the Iberian System extend from the eastern foothills of the Cantabrian Range; and the Betic System extends throughout the southern and eastern parts of Spain (Fig. 1).

Spain has great climate variability due to its complex orography and geographic situation (De Castro et al., 2005). The annual average values for mean air temperature increase from north to south (at equal altitudes) (Cantos and Molina, 2001), and range from below 2.5 °C in high altitude areas (Pyrenees) and to over 17 °C in the south and along part of the coastline between Malaga and Alicante. January is the coldest month of the year, while August is usually the hottest on the Cantabrian coast, in the Mediterranean and in the Gulf of Cadiz (Cantos and Molina, 2001). The Central Plateau and the Ebro and Guadalquivir depressions have their highest temperature in July. The average annual temperature decreases from south to north and from the coast inland (Cantos and Molina, 2001). It is worth noting that there is a difference of about 4 °C between the northern and southern coast and about 2 °C between the two plateaus (Font, 2000). The rainfall regime is characterized by its high spatial and temporal variability due to the complex orography and Spain's location between the Atlantic Ocean and the Mediterranean Sea (Serrano et al., 1999; Trigo and DaCamara, 2000; Morala et al., 2003). Annual precipitation values range from 300 mm/year in the coastal semi-desertic regions of the southeast (Romero et al., 1998), to over 1200 mm in the north-western provinces (Rodriguez-Puebla et al., 1998). Summer is the least rainy season.

2.2. Dataset of forest occurrence

Deciduous forests are the dominant type of vegetation in Eurosiberian territories, being their presence in the Mediterranean area of the Iberian Peninsula relatively scarce (Gavilán et al., 2018). The Eurosiberian region has Temperate macrobioclimate, characterized by the lack of summer drought. It means that the value in millimetres of the average rainfall for the hottest 2-month period in the summer quarter is more than twice the average temperature in degrees Celsius in the same period (Rivas-Martínez et al., 2017a). Deciduous forests are highlighted by the European Habitats Directive (EEC, 1992) as forest types of

Fig. 1. Study area.

Community importance. Member states are therefore obliged to take measures to maintain or restore the natural habitats and wildlife species listed in the Annexes of the Directive to a favourable conservation status.

The most characteristic and widespread Spanish deciduous forests are characterized by *Fagus sylvatica* (European beech), *Quercus robur* (pedunculate oak), *Quercus petraea* (sessile oak) and *Betula celtiberica* (Carpetan birch), which will be studied in this research. *Fagus sylvatica* forests are widely distributed across Europe and are among the most representative trees in the temperate deciduous forests of the Northern Hemisphere (Shen, 1992; Denk, 2003). This forest is of crucial importance to European biodiversity, as it provides a proper environment of a diverse array of plants, animals and other organisms (Geßler et al., 2006; Moning and Müller, 2009; Castaño-Santamaría et al., 2019). Oak species play an important ecological role as they support various types of insects, and their fruit (acorns) provide a valuable food source for many birds and mammals. The oak canopy allows significant light to penetrate, creating a diverse and enriched understory (Ducousso and Bordacs, 2004). *Quercus petraea* and *Quercus robur* are among the most economically and ecologically important deciduous forests in Europe (Ducousso and Bordacs, 2004). *Betula celtiberica* are endemic Iberian forests frequent in the Pyrenees, the Cantabrian Range and the northwest of the Iberian Peninsula, although their populations become scarce and more fragmented in the Iberian and Central systems (Álamo et al., 2010). According to the Worldwide Bioclimatic Classification System (WBCS, Rivas-Martínez et al., 2011a; Rivas-Martínez et al., 2017a), these forests can develop in the Iberian Peninsula in thermotemperate to lower orotemperate thermotypes and subhumid to ultrahyperhumid ombrotypes. It is worth noting that these Spanish deciduous formations represent the European southwestern limit of their distribution.

The Spanish deciduous forests belong to the class *Querco roboris-Fagetea sylvaticae*, which is one of the most widespread vegetation types in Spain. The class includes thermo- to lower orotemperate, meso-to lower oromediterranean subhumid to ultrahyperhumid and thermo-mesoboreal climatic deciduous broad-leaved and mixed broad-leaved *meso*-macroforests growing on many types of rich and poor soils. The canopy is mainly dominated by deciduous species of the genera *Quercus*

and *Fagus* (Rivas-Martínez et al., 2011b). 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; Annex I). In addition to this, Spain is a biodiversity hotspot (Médail and Quézel, 1997) and probably it has all the conditions to be severely affected by climate change (Benito Garzón et al., 2008). All these considerations make Spain an ideal place to carry out the present study.

The georeferenced distribution data for these forests were obtained from the map in the Habitats Directive 92/43/EEC and from the Forest Map of Spain (MFE50). The maps were rasterized using analytical tools and converted into points, which were located in the centre of all the cells using conversion tools implemented in ArcGis 10.7 (ESRI, 2010) for their subsequent application in SDMs. A minimum distance of 1 km between plots was considered to avoid the inclusion of spatial autocorrelation.

2.3. Predictor variables

2.3.1. Current conditions

Four categories of predictors were used in this study: bioclimatic, biogeographic, topographic, and soil variables. Temperature and precipitation data for the period 1979–2013 were collected from the CHELSA dataset (https://chelsa-climate.org/). CHELSA (climatologies at high resolution for the earth's land surface areas) is a high-resolution climate dataset (30 arc sec) for the earth's land surface areas (Karger et al., 2017). Several bioclimatic rasters were built from these climate data using Map Algebra implemented in ArcGis 10.7 (ESRI, 2010) and following the criteria of the Worldwide Bioclimatic Classification System (WBCS) (Rivas-Martínez et al., 2011a; Rivas-Martínez et al., 2017a). The WBCS essentially focuses on establishing a valid bioclimatic typology with an accurate relationship between climate values (parameters and bioclimatic indices) and vegetation models for the entire Earth. Bioclimatology can be used in programmes for the study and conservation of biodiversity or habitats, for making predictions in order to obtain agricultural and forestry resources and to determine future

climate and vegetation scenarios due to the high predictive value of bioclimatic units (Rivas-Martínez et al., 2011a).

We took into consideration the parameters and bioclimatic indices used to characterize plant communities and the following rasters were generated: **Tp** (positive annual temperature), **Pp** (positive annual precipitation), **Ic** (continentality index), **Io** (annual ombrothermic index), **Ios** (summer ombrothermic indices), **It** (thermicity index), **Itc** (compensated thermicity index) (Table S1).

Rivas-Martínez's bioclimatic classification system refers to the main climates, biomes and biogeographic units recognized on Earth. A biogeographic raster based on Rivas-Martínez et al. (2017b) was used in this study on this matter. Additional rasters such as digital terrain model (DTM), aspect, slope and soil (according to the FAO classification) were also included for modelling. All rasters were resampled at 500 m resolution.

2.3.2. Future projections

Topographic and soil predictors were considered to be unchanging, while for future climate variables we used the ones extracted by bias-corrected CMIP5 general circulation models (GMMs) for the period 2041–2060 (the 2050 s, medium term), available from the CHELSA climate dataset. CMIP5 is the fifth phase of the coupled model inter-comparison project (CMIP) promoted by the working group on coupled modelling (WGCM). To reduce the uncertainty arising from the single general circulation models (GCMs), we used four GCMs calibrated for the Northern Hemisphere and with satisfactory performance for Europe (McSweeney et al., 2015; Buras and Menzel, 2019): HadGEM2-ES, CCSM4, GDFL-CM3 and MPI-ESM-LR. These models have been also used by several authors in studies about climate change in Spain (Aparício et al., 2015; Amblar Francés et al., 2017; López-Tirado et al., 2018; Lopez-Tirado).

For each GCM we applied two representative concentration pathways (RCPs): RCP 4.5 and RCP 8.5. These emission pathways provide time- and space-dependent trajectories of concentrations of greenhouse gases and pollutants resulting from human activity, as adopted by the Fifth Assessment Report (AR5) (IPCC, 2014). The RCP 4.5 scenario stabilizes radiative forcing at 4.5 Wm − 2 in the year 2100, without ever exceeding that value, by employing technologies and strategies to reduce greenhouse gas emissions (GHG). RCP 8.5 is a more pessimistic scenario characterized by increasing GHG emissions and high GHC concentration levels. It represents a rising radiating forcing pathway leading to 8.5 Wm^{-2} in 2100 (approximately 1370 ppm CO_2 -equivalent) (Noce et al., 2017).

The same bioclimatic variables used to model the current conditions were built for each GCM and RCP for the period 2041–2060 using Map Algebra implemented in ArcGis 10.7 (ESRI, 2010).

2.4. Distribution modelling

The ensemble platform for species distribution models (Biomod2) (Thuiller et al., 2009) and RStudio v. 4.03 (R Core Team, 2019) was used to model the habitat suitability of the forests under both current conditions and climate change projections for the 2050 horizon (RCP 4.5 and RCP 8.5). Three commonly used algorithms were considered for modelling: maximum entropy (MaxEnt), random forest (RF) and generalised linear models (GLMs).

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). Two different statistical measures available in Biomod were considered in order to estimate the accuracy of the models: the area under the curve (AUC) of a receiver operating characteristic plot (ROC) and the true skill statistic (TSS). Although AUC has been criticized in some studies (Lobo et al., 2008; Jiménez-Valverde, 2012), it is the most commonly applied measure of accuracy for SDMs. Following Lobo et al. (2008) and Allouche et al. (2006), we also use TSS to evaluate the models and obtain information on their specificity and sensitivity.

Specificity reflects a model's ability to correctly predict an absence in a location, and sensitivity shows its ability to correctly predict a presence (Freeman and Moisen, 2008). The procedure was replicated 10 times for each forest, GCM and RCP to obtain more robust estimates of habitat suitability, thus generating a total of 320 single models (4 forests ×4 GCMs ×2 RCPs ×10 runs). The variable importance was calculated with the variable importance function implemented in the biomod2 package.

We then obtained ensemble forecasting models (one for each GCM, RCP and forest) by computing a consensus of single-model projections (Araújo and New, 2007; Marmion et al., 2009; Thuiller et al., 2009). The ensemble models were built giving higher importance to single models with a better performance according to the AUC and TSS criteria. Only models with AUC $\geq$ 0.9 and TSS $\geq$ 0.85 were chosen to create the ensemble models. The median probability of occurrence across the selected models for each grid cell was used.

A probability threshold that maximizes sensitivity and specificity was selected to transform the results of distribution modelling from probabilities to binary maps and differentiate suitable and non-suitable areas for forests studied. This method proved to be a good approach for threshold determination (Liu et al., 2005; Jiménez-Valverde and Lobo, 2007; Allouche et al., 2006). Maps of habitat suitability were imported into ArcGis 10.7 (ESRI, 2010).

At the end of the process, eight ensemble maps of habitat suitability (4 GCMs ×2 RCPs) were produced for each forest category. The next step was to combine them in two final suitability maps for each forest (one final map for RCP 4.5 and another for RCP 8.5). The approach proposed by IPCC-AR5 (Mastrandrea et al., 2011; Noce et al., 2017) was applied to deal with the uncertainty and communicate the likelihood of the outcomes. If the suitability is predicted by only one GCM the outcome is considered "unlikely", by two GCMs it is "moderately likely", by three GCMs "highly likely" and by four GCMs "totally likely". The results of these maps will be complemented with results of the analysis of range change mentioned in the subsection below.

2.5. Analysis of changes

2.5.1. Distribution

The maintenance, expansion (gain) or reduction (loss) of habitat suitability was calculated for each forest under the climate change projections. The percentage of predicted future range change (C) by cell was also estimated according to Hu et al. (2011) as follows:

C = 100* (RG-RL)/PR, where RG (range gain) is the number of grid cells projected in 2050 as being unsuitable under current conditions but suitable in 2050; RL (range loss) is the number of grid cells projected as suitable under current conditions but unsuitable in 2050; and PR (present range) is the number of grid cells projected as suitable under present conditions. A positive C value means an increase in overall range size and a negative value indicates a loss.

The data on changes in range size for each forest is complemented with information on the likelihood of the outcomes.

2.5.2. Vulnerability

The vulnerability of the Spanish deciduous forests under climate change was analysed applying the Vulnerability Index proposed by Felicísimo et al. (2012). The Vulnerability Index (VI) is defined as follows:

VI = 1-((FPA ∩ COA)*(FPA ∩ CPA)) where:

FPA ∩ COA is the intersection of the future potential area (in surface units) and the current occupied area in the whole study area, and FPA ∩ CPA is the intersection of the future potential area (in surface units) and the current potential area. The degree of vulnerability can be used as an indicator to define priorities in conservation policies. According to these authors the levels of vulnerability are:

VI < 0.00: No vulnerability
VI < 0.4: Low vulnerability
VI (0.4–0.7): Medium vulnerability

VI (0.7–0.85): High vulnerability

VI (0.85–0.95): Very high vulnerability

VI > 0.95: Critical vulnerability

A new vulnerability range is proposed in this study: VI: 0.01–0.1 (Very low vulnerability). The vulnerability analysis was carried out at the level of biogeographic subprovince as the impacts of climate change may be different in deciduous forests, as will be discussed below.

3. Results and discussion

3.1. Current conditions

Table 1 shows the average measures for 10 runs to test the predictive performance of SDMs under current climate conditions. The AUC and TSS for the single models indicated excellent (for AUC) and good to excellent (for TSS) model performance for all the forests studied. The overall accuracy in terms of averages among the metrics is between 0.93 (*Q. robur* and *B. celtiberica*) and 0.97 (*Q. petraea*). These results mean that the distributions of deciduous forests in Spain are well described by the selected predictors, making them suitable for deriving future projections. Based on the AUC and TSS results, all single models were included for the final ensemble forecasting models.

Table 2 shows the importance of the predictors selected in this study. Six variables have the highest contribution to the single models. The continentality index (Ic), ombrothermic index of the two hottest months of the summer quarter (Ios$_2$) and biogeography are the predictors with the strongest influence on the distribution of all the forests analysed. The importance of ombrothermic indices for characterizing and delimiting the distribution of deciduous forests has previously been reported by del Río et al. (2005a), del Río et al. (2018). The incorporation of biogeography in species distribution models produced good results in several previous investigations (Alfaro-Saiz et al., 2015; del Río et al., 2018). The findings of this study are also in line with Castaño-Santamaría et al. (2019), who reported that isothermality is a key variable for the distribution of beech forests in the Cantabrian Range. Fang and Lechowicz (2006) also pointed out that continentality contributes to the distribution of European beech.

The compensated thermicity index (Itc) also appears to be crucial for the occurrence and distribution of *Fagus sylvatica* and *Quercus petraea* forests. This bioclimatic index takes into consideration the temperatures (maximum and minimum) of the coldest month of the year. Our results are in agreement with Fang and Lechowicz (2006) and Casalegno et al. (2011) who described the role of the minimum temperature of the coldest month for modelling the suitability of European forests. The same authors concluded that summer temperature is a limiting factor for the distribution of *Fagus sylvatica*. Accordingly, Roces-Díaz et al. (2014) confirmed that winter temperature is the main factor affecting the distribution of *Fagus sylvatica* and *Quercus petraea* forests in SpainThe annual ombrothermic index (Io) and the ombrothermic index of the hottest month of the summer quarter (Ios$_1$) appear to be decisive for the distribution of *Quercus robur* and *Betula celtiberica*.

Fig. 2 shows the biogeographic units where deciduous forests can occur in Spain, and Fig. 3 displays the potential suitable areas for their distribution under current conditions based on the results obtained with SDMs.

The current potential suitable areas for *Fagus sylvatica* extend up to 26591.1 km^2 (Fig. 3a) revealing a strong preference for the meso and supratemperate humid-hyperhumid territories in the Pyrenees, Cantabrian Range, Basque mountains and the Iberian System. These areas belong to the Orocantabrian, Cantabrian Atlantic and Central Pyrenean biogeographic subprovinces, and the northern zones of the East Pyrenean and Oroiberian subprovinces. The southernmost beech forests are found in two small areas in the Central System and Beceite Pass, all of which have Temperate macrobioclimate with submediterranean bioclimatic variant, meaning that precipitation (P) in at least one month of the summer period is <2.8 T (mean temperature).

Current suitable areas for *Quercus petraea* forests (14540.9 km^2) (Fig. 3b) mostly occur in the supratemperate humid and hyperhumid bioclimatic belt of the Cantabrian Range (Orocantabrian and Cantabrian Atlantic subprovinces). There are also small locations in the east of Spain (East Pyrenean and Catalonian and Provençe subprovinces).

Quercus robur forests are widely extended along the whole Cantabrian Atlantic subprovince, covering an extension of 51508.5 km^2 (Fig. 3c). They have a strong preference for the mesotemperate thermotype and the humid ombrotype. Lesser areas may be also located in the Pyrenees (Central and East Pyrenean subprovinces).

The most suitable areas for *Betula celtiberica* forests are situated in the Cantabrian Range (Orocantabrian and Cantabrian Atlantic subprovinces), occupying an extension of 20426.2 km^2 (Fig. 3d). There are also potential zones for these forests in the Pyrenees (Aragón Prepyrenean and Central and East Pyrenean subprovinces). They are dominant in the meso and supratemperate thermotypes with humid and hyperhumid ombrotypes.

Results reported in this study agrees with the known distribution of this type of vegetation and the Rivas-Martínez potential vegetation map (Rivas-Martínez, 1987).

3.2. Future projections

Several studies carried out in the last decade have reported generalized increases in temperature and a decline in rainfall for Spain: del Río et al. (2005b), del Río et al., 2011a, del Río et al. (2011b), del Río et al. (2012), González-Hidalgo et al. (2011), Gonzalez-Hidalgo et al. (2020), Ríos Cornejo et al. (2012), Ríos Cornejo et al. (2013), Sandonis et al. (2021). These trends also imply changes in the bioclimatic indices studied in this research, which are more noticeable under the RCP 8.5 scenario. A generalized future downward trend in the values of ombrothermic indices (annual and summer ones) has been confirmed in this study. The most significant drops in the summer ombrothermic indices (Ios) could occur in the Pyrenean subprovinces, and the smallest in the Cantabrian Atlantic subprovince (especially in its western areas). Slight increases in these variables have indeed been observed in the Orocantabrian subprovince. Ios are very useful indices to delimit the frontier between the Mediterranean and Temperate macrobioclimates and to establish the submediterranean variant in temperate areas (Rivas-Martínez et al., 2011a). Decreases in the summer ombrothermic indices could imply a reduction in the extension of the Temperate macrobioclimate, with significant effects on the distribution of the forests in the study. Positive temperature (Tp) and compensated thermicity index (Itc) values will increase in future compared to current data, due to rising temperatures. The magnitude of these increases will differ depending on the biogeographic unit. The steepest rises in these

Table 1

Summary of measures for AUC and TSS.

Taxon	AUC			TSS			OVERALL ACURACY
	Average	Sensitivity	Specificity	Average	Sensitivity	Specificity	Average
Betula celtiberica	0.97	0.98	0.90	0.88	0.98	0.90	0.93
Fagus sylvatica	0.98	0.98	0.93	0.91	0.98	0.94	0.95
Quercus petraea	0.99	0.98	0.96	0.94	0.98	0.97	0.97
Quercus robur	0.97	0.98	0.90	0.88	0.98	0.90	0.93

Table 2

Variables importance.

Predictors	F. sylvatica	Q. petraea	Q. robur	B. celtiberica	Average	SD
Altitude	0.011	0.017	0.061	0.061	0.038	0.027
Aspect	0.012	0.008	0.006	0.005	0.008	0.003
Biogeography	0.120	0.178	0.113	0.204	0.154	0.045
Ic	0.253	0.569	0.264	0.307	0.348	0.149
Io	0.016	0.075	0.147	0.113	0.088	0.056
Ios_1	0.101	0.128	0.116	0.110	0.114	0.011
Ios_2	0.175	0.446	0.092	0.086	0.200	0.169
Ios_3	0.072	0.152	0.035	0.052	0.078	0.052
Ios_4	0.018	0.252	0.030	0.024	0.081	0.114
Itc	0.171	0.222	0.047	0.056	0.124	0.086
Slope	0.019	0.025	0.009	0.007	0.015	0.009
Soil	0.016	0.082	0.051	0.080	0.057	0.031
Tp	0.047	0.024	0.026	0.030	0.032	0.011

Ic: continentality index; Io: annual ombrothermic index; Ios_1, Ios_2, Ios_3, Ios_4: summer ombrothermic indices; Itc: compensated thermicity index; Tp: annual positive temperature; SD: Standard deviation.
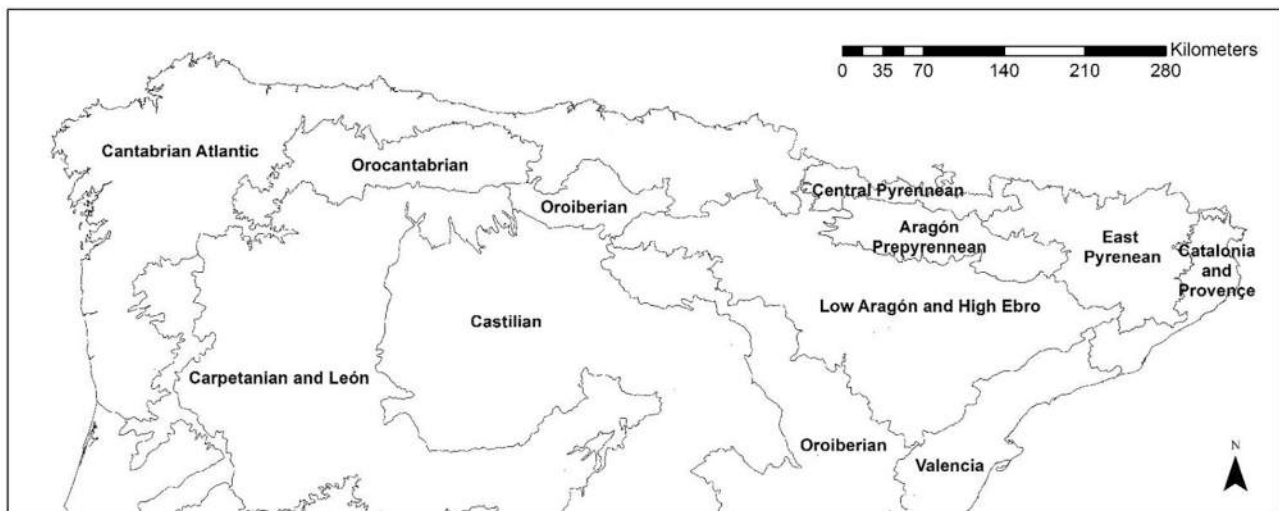

Fig. 2. Biogeographic subprovinces.

variables could occur in the Aragón Prepyrenean subprovince, and the lowest in the Orocantabrian subprovince and the western areas of the Cantabrian Atlantic subprovince. An increase in continentality can also be seen all over Spain in both RCPs in the future being more acute in the Pyrenean subprovinces than in the Orocantabrian and Cantabrian Atlantic subprovinces.

The reported trends in the abovementioned bioclimatic indices are essential for understanding possible changes in the habitat suitability of Spanish deciduous forests due to climate change.

3.2.1. Changes in distribution

Eight maps of habitat suitability (4 GCMs ×2 RCPs) were generated for each forest category. They were then combined into two single suitability maps (one for RCP 4.5 and another for RCP 8.5) to obtain the maps of the future likelihood of habitat suitability for both emission pathways (Fig. 4). In general, the study reveals unlikely outcomes (suitability predicted by one GCM) for the forests located in the southernmost areas, mostly coinciding with the limit between the Temperate and Mediterranean macrobioclimates (with exceptions for *Fagus sylvatica* and *Quercus robur* forests). The best likelihood values (suitability predicted by three or four GCMs) were found for *Fagus sylvatica* (Fig. 4a) and *Quercus robur* forests (Fig. 4c) in the Cantabrian Range (Orocantabrian subprovince) and in the northwest of the Cantabrian Atlantic subprovince. *Betula celtiberica* formations only have a high likelihood of suitability in the Pyrenees and the Cantabrian Range under the RCP 4.5 scenario, but this drastically decreases in the RCP 8.5 projection

(Fig. 4d).

Fig. 5 shows the predicted changes in habitat suitability under RCP 4.5 and RCP 8.5 scenarios compared to current conditions, and Table 3 displays the kilometres gained, lost and maintained. The Wilcoxon signed-rank test was used to verify statistically significant differences in habitat suitability between current and future conditions assuming 95% confidence level.

The total loss of suitable areas for *Fagus sylvatica* forests is 17.6%, although it is worth noting that the results differ depending on the location (Fig. 5a). Beech forests could suffer a loss of overall range in areas mostly located at their southern limit of distribution close to the frontier with the Mediterranean macrobioclimate, in the Aragón Prepyrenean and East Pyrenean subprovinces, and in the Oroiberian subprovince. Our results are in line with other authors who also reported that the southernmost positions occupied by these forests will decrease or disappear under climate change scenarios (Ellenberg, 1988; Jump et al., 2006; Felicísimo et al., 2012; Ruiz-Labourdette et al., 2013; Castaño-Santamaría et al., 2019). This loss of suitability is likely related to the abovementioned reduction in the extension of the Temperate macrobioclimate and the sensitivity of these forests to summer droughts (Scharnweber et al., 2011; Dulamsuren et al., 2017; Noce et al., 2017). Numerous dendrochronological and ecophysiological studies suggest that *Fagus sylvatica* is more drought sensitive than other broad-leaved species, such as *Quercus petraea* and *Quercus robur* (Knutzen et al., 2015; Dulamsuren et al., 2017). European beech responds to soil watershortage with reductions of stomatal conductance (Köcher et al.,
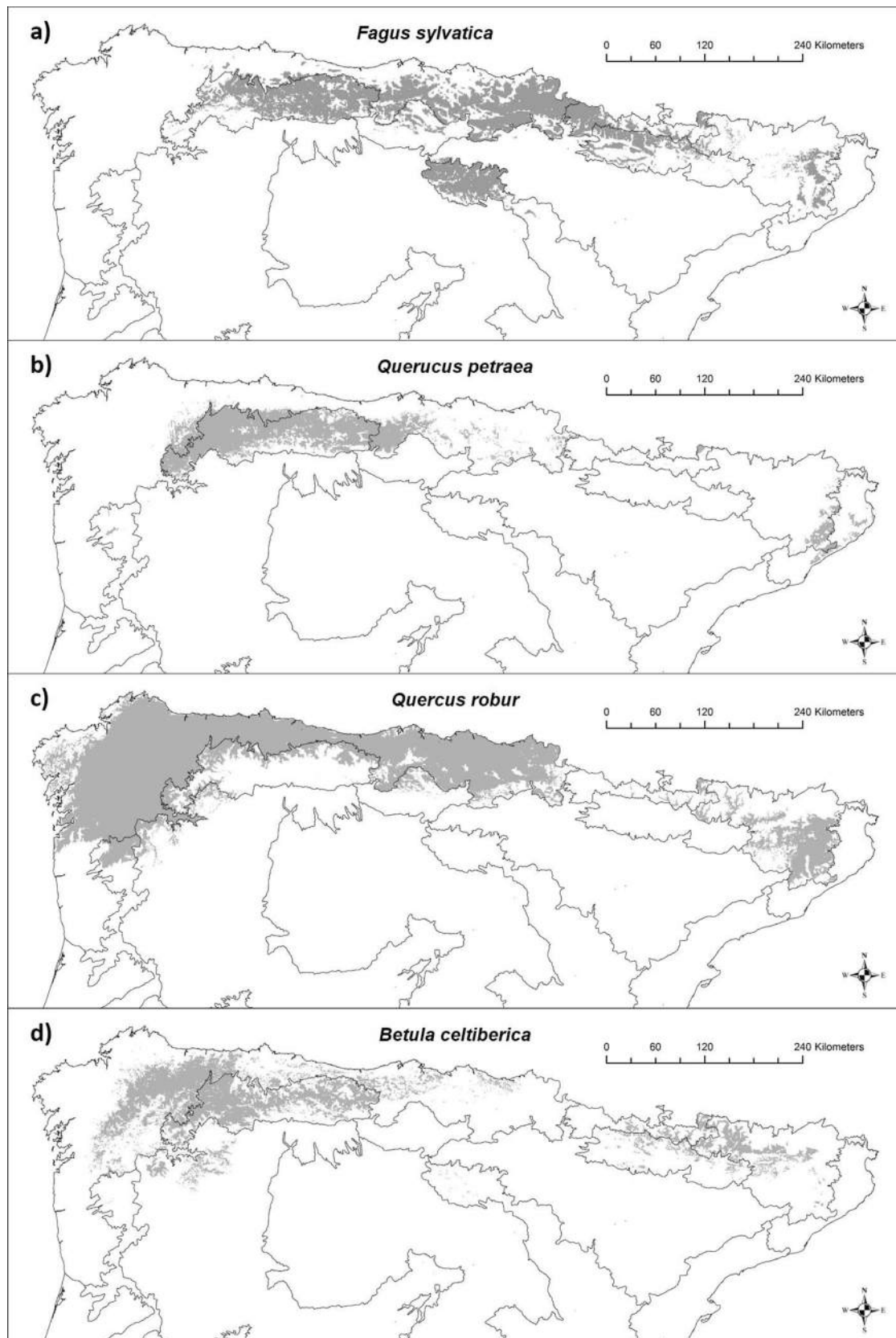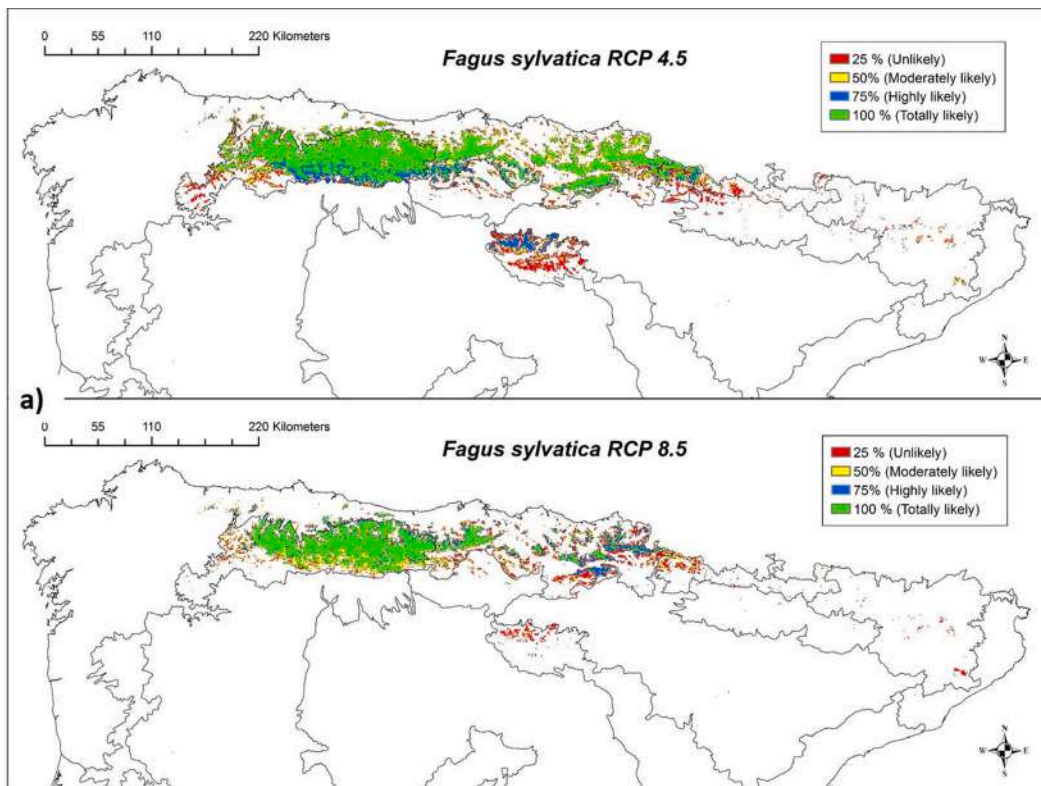
Fig. 3. Habitat suitability maps under current conditions (shaded in grey). **a)** *Fagus sylvatica*, **b)** *Quercus petraea*, **c)** *Quercus robur*, **d)** *Betula celtiberica*.
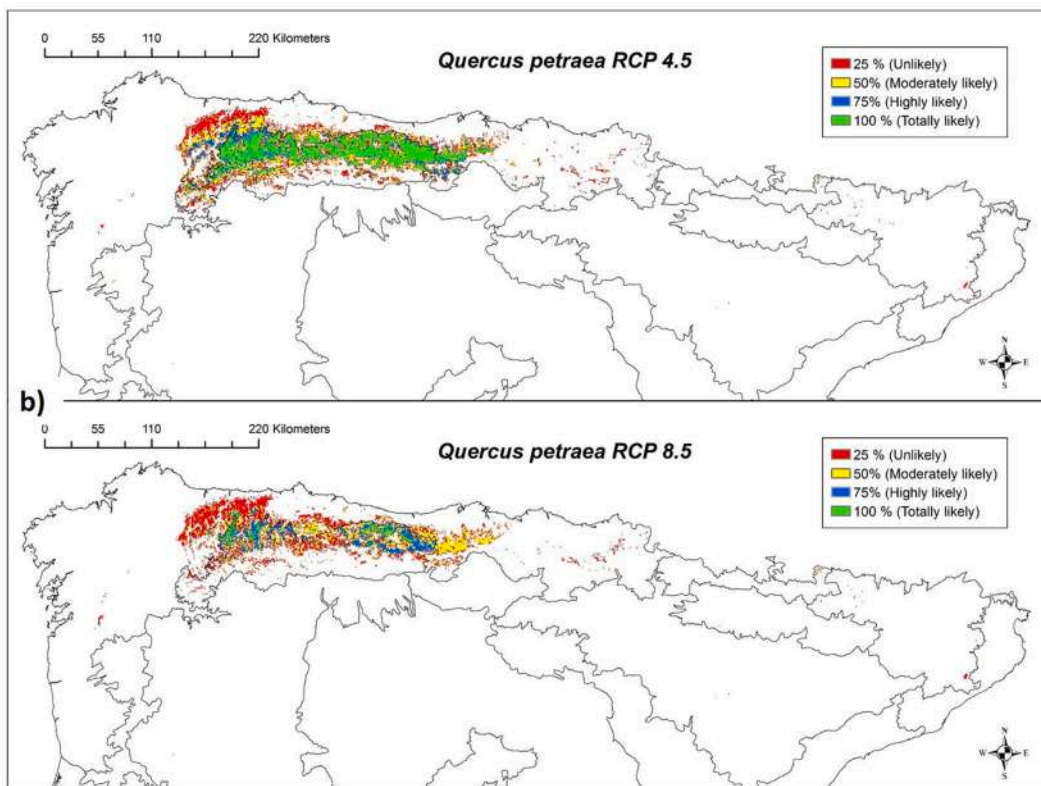
491

492

22

Fig. 4. Future likelihood suitability for deciduous forests under RCP 4.5and RCP 8.5 scenarios. **a)** *Fagus sylvatica*, **b)** *Quercus petraea*, **c)** *Quercus robur*, **d)** *Betula celtiberica.*
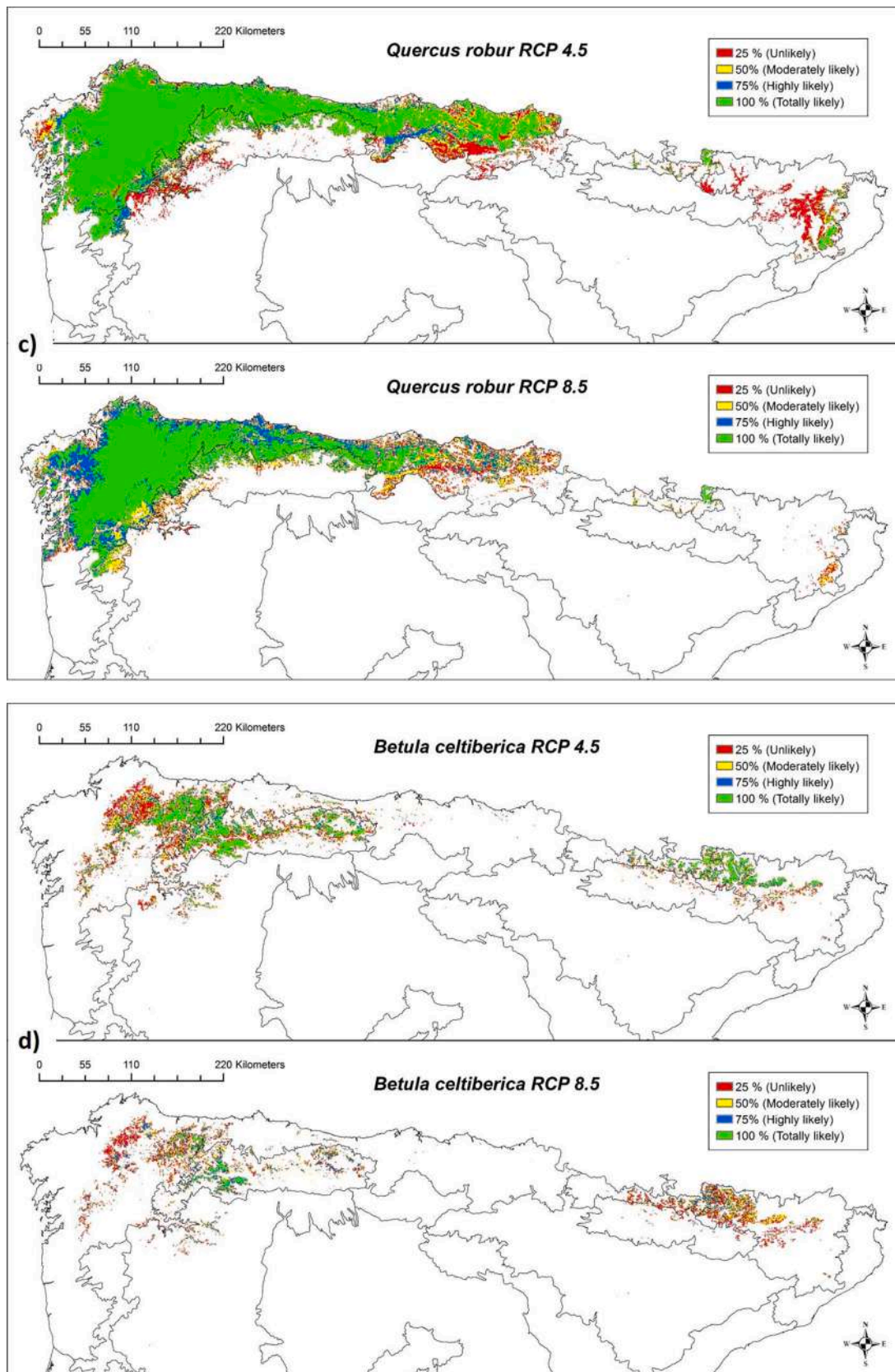
Fig. 4. (*continued*).

2009); vulnerability to cavitation in the conducting system (Bréda et al., 2006); increase fine root mortality and turnover (Leuschner et al., 2001; Hertel et al., 2013) and pre-senescent leaf shedding (Jump et al., 2006;

Granier et al., 2007), among other effects. The suitability loss could lead to rather lower levels of regeneration (Silva et al., 2012); higher risk of mortality of trees (Allen et al., 2010; Aranda, 2015); decrease in the
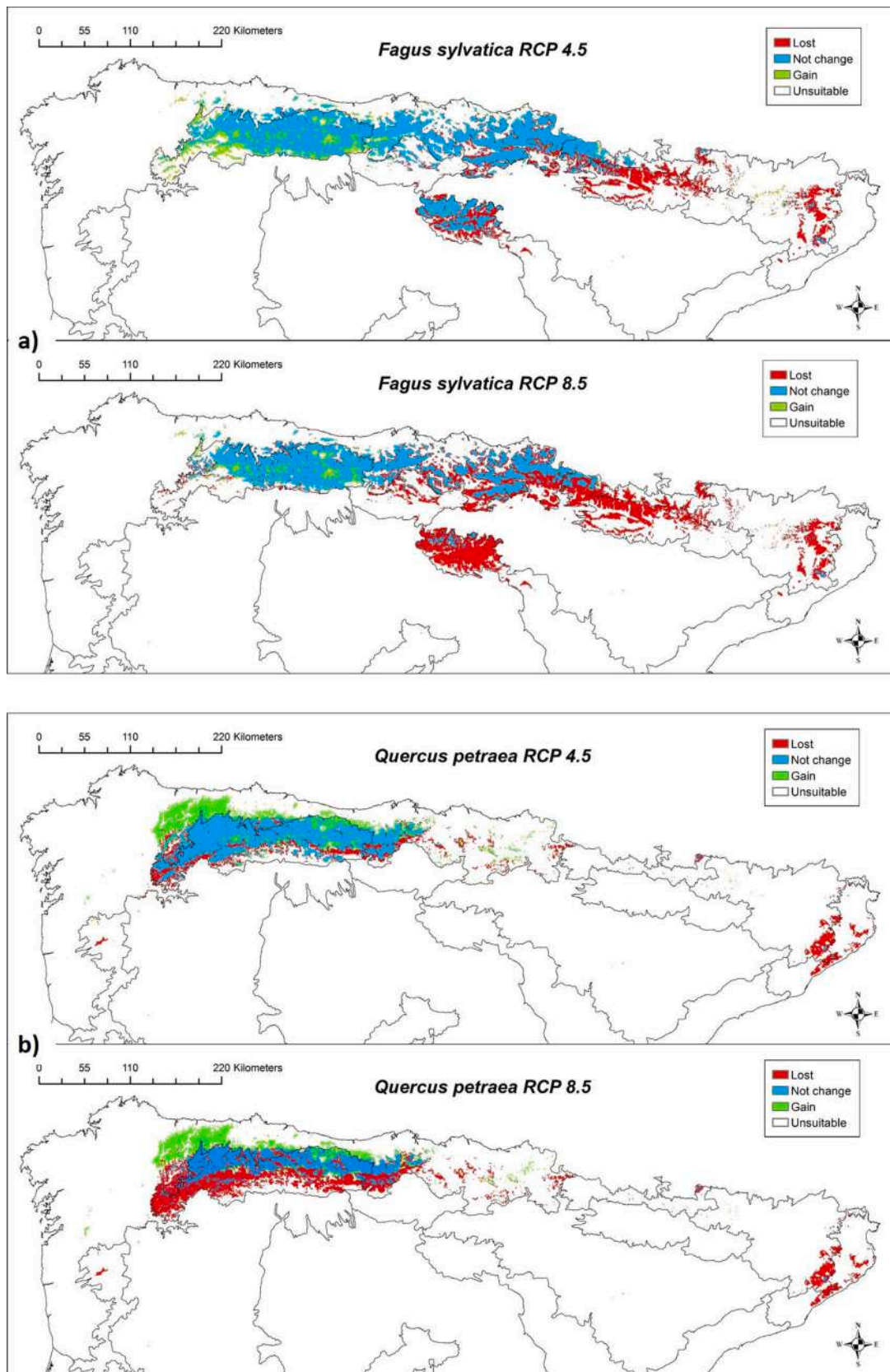
Fig. 5. Loss, maintenance and gain of suitable areas for deciduous forests under RCP 4.5 and RCP 8.5 scenarios. **a)** *Fagus sylvatica*, **b)** *Quercus petraea*, **c)** *Quercus robur*, **d)** *Betula celtiberica.*
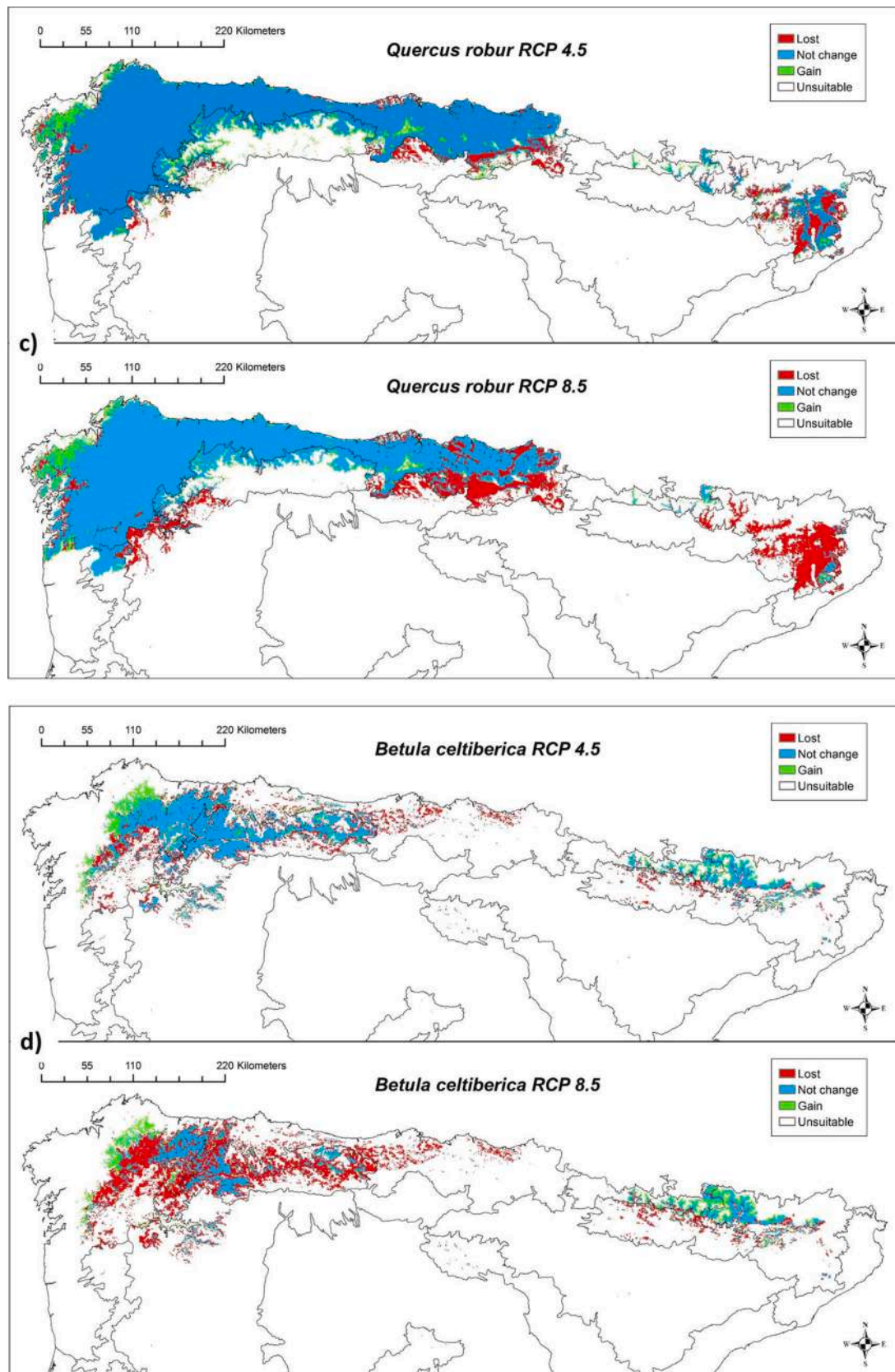
Fig. 5. (*continued*).

growth of adult trees at the lower limit distribution (Jump et al., 2006); reduction in local diversity (Falk and Hempelmann, 2013); less favourable conditions for seedling establishment (Castaño-Santamaría et al., 2019); changes in leave unfolding and fall (Peñuelas et al., 2002) or changes in recruitment patterns (Jump et al., 2006; Peñuelas et al., 2007).

Table 3
Predicted changes in habitat suitability for deciduous forests under climate change scenarios.

FOREST	CURRENT	RCP 4.5				RCP 8.5			
	Predicted km^2	Predicted km^2	Maintained km^2	Increased km^2	Reduced km^2	Predicted km^2	Maintained km^2	Increased km^2	Reduced km^2
Fagus sylvatica	26591.1	21905.7	18490.4 (69.6%)	3415.37 (12.8%)	4685.31 (17.6%)	13920.9	12554.4 (47.2%)	1366.6 (5.2%)	12663.8 (47.6%)
Quercus petraea	14540.9	13881.1	9782.1 (67.3%)	4099.02 (28.2%)	659.81 (4.5%)	9716.7	6145.7 (42.3%)	3571 (24.6%)	4812.5 (33.1%)
Quercus robur	51508.5	49437.7	45128.3 (87.6%)	4309.37 (8.4%)	2070.83 (4.0%)	40645.6	38038.2 (73.9%)	2607.4 (5.1%)	10800.4 (21%)
Betula celtiberica	20426.2	15657.7	12943.1 (63.4%)	2714.67 (13.3%)	4768.46 (23.3%)	9235.6	6859.9 (33.6%)	2375.7 (11.6%)	11193.4 (54.8%)

Our study provides some hope in the face of such pessimistic outlook for beech forests in the western areas of the Orocantabrian subprovince, where *Fagus sylvatica* formations may increase their distribution, thus guaranteeing the suitability of their habitat in future (25–50% likelihood, Fig. 4a). This result may be associated with rises in the ombrothermic indices in these areas (del Río et al., 2005a; del Río et al., 2018). Muñoz-Sobrino et al. (2008) also identified increases in the niche of *F. sylvatica* from the late Medium Holocene in the northwest of the Iberian Peninsula due to the rise in the elevation of the tree line in the Cantabrian Mountains. This has led to a migration towards higher altitudes (approximately 100 m compared to current conditions) and a northward shift, both associated with increases in positive temperature and the compensated thermicity index in future. Sanz-Elorza et al. (2003), Thuiller (2003), Lindner et al. (2010), Roces-Díaz et al. (2014), Weigel et al. (2018), Buras and Menzel (2019) and Castaño-Santamaría et al. (2019) also reported shifts to northern latitudes and higher altitudes in these forests.

The impact of climate change on the future distribution of *Quercus petraea* forests could imply losses in their overall range in the southernmost part of the Orocantabrian subprovince and in the East Pyrenean and Catalonian and Provençe subprovinces (Fig. 5b, Table 3), while suitable new areas could occur in the central and western territories of the Cantabrian Atlantic subprovince (likelihood 25%-50%, Fig. 4b). This result could be associated with the shift to occupy northern areas caused by higher temperatures.

At the national scale, no future problems are expected to occur with *Quercus robur* forests due to climate change, since 87.6% could preserve their potential areas in 2050 (Fig. 5c, Table 3). The highest losses are found for the Pyrenean forests, coinciding with the results reported by Felicísimo et al. (2012). Suitable new areas for these forests could occur in the Orocantabrian subprovince and in the westernmost areas of the Cantabrian Atlantic subprovince (likelihood 75%-100%, Fig. 4c). A slight migration to higher altitudes (approximately 30 m in relation to current conditions) associated with increases in the mean temperature and the continentality index has been also observed. These results are consistent with other authors who reported that *Quercus robur* may benefit from climate change in some parts of Europe (Noce et al., 2017; Perkins et al., 2018).

The greatest losses of habitat suitability under the RCP 4.5 projection could affect *Betula celtiberica* forests (Fig. 5d, Table 3), whose future distribution could be reduced by up to 23.3% compared to current conditions. The main decreases can be observed at the southern edges of their distribution area close to the frontier with the Mediterranean macrobioclimate in all biogeographic units. Noce et al. (2017) also reported drastic reductions in their range distribution in southern Europe. A migration towards higher altitudes (approximately 100 m higher than at present) and a northward shift into new areas is expected in the Pyrenees (likelihood 100%, Fig. 4d) and in the northwest of the Cantabrian Range (likelihood 25%-50%, Fig. 4d). The same tendency to migrate to northern areas has been noted by Hemery et al. (2010) for these forests in Europe.

The changes identified under the RCP 4.5 projection will be accentuated in the RCP 8.5 scenario. Suitable areas for *Fagus sylvatica* could be reduced by up to 47.6% compared to current conditions at the national scale due to its drastic reduction (practical disappearance) in the Iberian System (Oroiberian subprovince) and the Pyrenees (Pyrenean subprovinces) (Fig. 5a, Table 3). These forests may only survive in future in the Cantabrian Range (Orocantabrian subprovince) (likelihood 75–100%, Fig. 4a) and the eastern areas of the Cantabrian Atlantic subprovince (likelihood 75–100%, Fig. 4a).

Quercus petraea forests may persist in suitable areas to the north of the Orocantabrian subprovince (Fig. 5b, Table 3) with likelihood values of about 75–100% (Fig. 4b). New distribution areas for sessile oaks (although with low probability) could be located in central and southern areas of the Cantabrian Atlantic subprovince due to their northward migration.

Quercus robur forests may be the least affected by climate change in Spain (Fig. 5c, Table 3) as has been mentioned for the RCP 4.5 projection. Benito Garzón et al. (2008) also pointed out that *Quercus robur* will not undergo a drastic decline under future climate change scenarios. Pedunculate oak forests may preserve their habitat suitability throughout 74% of their current distribution, and have their main extension in the central and western territories of the Cantabrian Atlantic subprovince (likelihood >75%, Fig. 5c). Gains are also projected with a high level of likelihood in the westernmost territories of this biogeographic unit as reported for the RCP 4.5 scenario. Losses of suitability are observed in the southern part of the Cantabrian Atlantic and East Pyrenean subprovinces.

Betula celtiberica forests could suffer the largest losses (up to 54.8%) and changes in their future distribution. A drastic reduction in suitable areas could occur in the Cantabrian Atlantic and Orocantabrian subprovinces, and they could disappear from the Oroiberian subprovince (Fig. 5d, Table 3). A northward shift and a migration to higher altitudes (approximately 250 m higher than at present) is expected in the Central and Eastern Pyrenean subprovinces (likelihood 25%-50%, Fig. 4d). This result agrees with the trend reported by Hemery et al. (2010) for these forests in Europe.

In summary, the percentage of predicted future range change for RCP 4.5 and RCP 8.5 emission pathways generally reveals negative values (indicating a loss in overall range) except for *Fagus sylvatica* and *Quercus robur* forests in the Orocantabrian subprovince and *Quercus petraea* in the Cantabrian Atlantic subprovince. The areas lost by deciduous forests could be occupied by sub-mediterranean or evergreen species (*Quercus sp.*), which are currently undergoing a northward expansion, as has been reported in southern Europe (Peñuelas and Boada, 2003; Gritti et al., 2006; Thuiller et al., 2006; Guiot and Cramer, 2016; Lindner et al., 2010; Ruiz-Labourdette et al., 2013).

3.2.2. Vulnerability

Table 4 shows the results of the vulnerability analysis following Felicísimo et al. (2012). Our data confirm, in line to that commented in previous sections, that the levels of vulnerability differ depending on the biogeographic unit and the type of forest analysed, and are always worse for the RCP 8.5 scenario. No vulnerability is expected for the

Table 4
Vulnerability for the studied forests under climate change scenarios according to Felicísimo et al. (2012).

	RCP 4.5						RCP 8.5						
	OC	CA	PY	OB	CL	CP	OC	CA	PY	CP	OB	CL	CP
Fagus sylvatica	No	Low	Very high	Medium	NA	NA	No	Medium	Critical	NA	Critical	NA	NA
Quercus petraea	Low	Low	Critical	NA	Critical	NA	Medium	Medium	Critical	NA	NA	Critical	NA
Quercus robur	No	Very low	Medium	NA	NA	NA	Very low	Low	Critical	NA	NA	NA	NA
Betula celtiberica	Low	Medium	Medium	Critical	NA	Critical	High	Very high	Medium	Critical	Critical	NA	Critical

OC: Orocantabrian subprovince, CA: Cantabrian Atlantic subprovince, PY: Pyrennean subprovinces, OB: Oroiberian subprovince, CL: Catalonian and Provençe subprovince, CP: Carpetanian and León subprovince. NA: The forest does not occur in the biogeographic unit.

Orocantabrian *Fagus sylvatica* forests, as increases in the overall range were observed for both RCP 4.5 and RCP 8.5 and the current populations could be maintained in future with high percentages of probability. The most vulnerable beech forests are located in the Pyrenean subprovinces showing very high (RCP 4.5) and critical vulnerability (RCP 8.5). The *Quercus petraea* forests least affected (low to medium vulnerability) correspond to those belonging to the Orocantabrian and Cantabrian Atlantic subprovinces, while the Pyrenean forests are the most sensitive (with critical vulnerability for both RCPs). *Quercus robur* formations occurring in the Orocantabrian subprovince are expected not to be vulnerable under RCP 4.5 and their vulnerability will be very low under the RCP 8.5 projection. The most sensitive pedunculate oak forests are in the Pyrenees, showing a critical status in the most pessimistic scenario (RCP 8.5). As mentioned above, the Spanish deciduous forests most severely affected by climate change are those of *Betula celtiberica*. Vulnerability could be very high in the Cantabrian Atlantic subprovince (RCP 4.5), while the lowest values were observed in the Pyrenean subprovinces.

In summary, and generally speaking, Orocantabrian and Cantabrian Atlantic forests could be the Spanish deciduous communities least affected by climate change, while the Pyrenean and Oroiberian forests could suffer the greatest losses of habitat suitability. These results seem to be related to trends reported in bioclimatic variables such as the summer ombrothermic indices (Ios) and continentality. To that effect, the most significant drops in Ios will occur in future in the Pyrenean subprovinces, and the smallest in the Cantabrian Atlantic subprovince. Slight increases in these bioclimatic variables have indeed been observed in the Orocantabrian subprovince (especially in its western areas). These results agree with del Río et al. (2005a), del Río et al. (2018). In addition to this, the tendency to increase the continentality in the Pyrenean at higher rates than in the Orocantabrian and Cantabrian Atlantic subprovinces could be associated with a greater loss of suitability of Pyrenean forests in comparison with Orocantabrian and Cantabrian Atlantic ones.

4. Conclusions

Species distribution models (SDMs) are a useful tool to assess the impact of climate change on species that require monitoring and management. In this study, we analysed the current and future habitat suitability of the main Spanish deciduous forests using an ensemble forecasting approach, with three different SDM algorithms, four GCMs and two representative emission pathways. The latest approaches in bioclimatology and biogeography were combined with topographic and soil variables and used as predictors to build the models. Vulnerability analysis is also carried out.

Although SDMs inevitably include some degrees of uncertainty related to the inherent variability of natural systems (Gould et al., 2014; Porfirio et al., 2014; Taleshi et al., 2019; Noce et al., 2019), the AUC and TSS results obtained in this research reveal that the distribution of the forests in the study area are well described by the selected predictors, making them suitable for deriving future projections and providing important information on their habitat suitability and vulnerability under climate change scenarios.

The continentality index (Ic), the ombrothermic index of the two hottest months of the summer quarter (Ios$_2$), and biogeography are the predictors with the strongest influence on the distribution of all the forests studied. The compensated thermicity index (Itc) also appears to be decisive for the occurrence and distribution of *Fagus sylvatica* and *Quercus petraea* forests.

The results revealed generalized losses in habitat suitability compared to present conditions for all the forests analysed, and were more acute for the RCP 8.5 projection. The exceptions were *Fagus sylvatica* and *Quercus robur* forests in the Orocantabrian subprovince and *Quercus petraea* in the Cantabrian Atlantic subprovince. The data on changes in the range size were complemented with information on likely suitability according to the IPCC terminology.

The vulnerability analysis confirmed that the deciduous forests least affected by climate change in future will be the Orocantabrian forests, while the Pyrenean and Oroiberian are the most vulnerable. It is worth emphasizing the importance and usefulness of conducting vulnerability analyses at the biogeographic level, as they will require different management and conservation policies depending on the results obtained.

The drastic reduction predicted in the habitat suitability of Spanish deciduous forests highlights the serious potential impact of climate change in Spain, and may also affect European diversity since the Iberian Peninsula is a biodiversity hotspot. The study reveals the importance and usefulness of these analyses at the biogeographic level, since the impacts of climate change differ depending on the deciduous forest analysed. In this line, the authors consider that the results of this study can offer basic information for decision-makers and serve as a useful tool to develop plans for the conservation and management of these forests in order to mitigate the impact of climate change and help conserve their benefits for society.

CRediT authorship contribution statement

S. del Río: Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Software, Visualization, Writing - original draft, Writing - review & editing. **R. Canas:** Data curation, Visualization. **E. Cano:** Writing - review & editing. **A. Cano-Ortiz:** Data curation, Visualization. **C. Musarella:** Data curation, Resources, Visualization. **C. Pinto-Gomes:** Writing - review & editing. **A. Penas:** Conceptualization, Visualization, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108202.

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