Distribution of *Eucalyptus globulus* Labill. in northern Spain: contemporary cover, suitable habitat and potential expansion under climate change

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Abstract

The goals of this study were to analyze the current status of eucalypt plantations in northern Spain and to assess current and future potential expansion of these plantations under climate change. The findings showed that the area occupied by *Eucalyptus globulus* has increased greatly (by 4.6 times) in northern Spain in the last 50 years, to reach the current cover of 389033.57 ha. This area represents 18.22% of the total area of wooded land, although the proportion varies widely in different provinces (0.28% in the inland province of Ourense and 44.76% in A Coruña). In order to assess the current and future species distribution for two climate change scenarios, species distribution models were fitted to data on 53 spatially-continuous environmental variables (terrain, climate, soil and hydrographical variables) derived from 3014 plots with presence of eucalypts and included in the third Spanish national forest inventory. The Random Forest machine learning method proved to be the best approach for modelling eucalypt occurrence, which was found to be related to 18 variables. Climate, soil and terrain were the most important variables in the model (explaining respectively 51.2%, 34.2% and 10.1% of the variation). Future projections were made for 2050 and 2070 by considering representative concentration pathway (RCP) scenarios 4.5 and 8.5 and applying the BCC-CSM1.1 model of the IPCC's 5th Assessment Report, which forecasted a significant increase in the suitable habitat in the inland areas of Galicia (northwest Spain) and a slight reduction in the other three autonomous communities in northern Spain (Asturias, Cantabria and Euskadi). The current suitable habitat in forest land and other natural and seminatural areas (SH_{NET}) includes an area of 830885.41 ha available for potential expansion of eucalypt, of which a total of 296356.71 ha is currently occupied by native broadleaved forest, mainly in Galicia (185420.12 ha). In addition, an increase in SH_{NET} of up 398810.27 ha is expected by 2070 in the worst climate change scenario (RCP 8.5), so that pressure on the native forest will mainly increase in the inland areas of Galicia. In natural protected areas, eucalypts currently occupy an area of 7840.40 ha, which represents 7.10% of the SH_{NET} included in natural protected areas in the study zone (110428.78 ha). The largest such area (5032.65 ha) is in Galicia and represents 7.42% of the SH_{NET} in natural protected areas in the region (67836.64 ha). In the future, this amount will increase by between 59.16% and 87.89% in Galicia but will decrease by between 18.41% and 30.59% in the other autonomous communities in northern Spain, with the exception of the RCP 8.5 scenario for 2070, in which an increase of 4.42% is forecast. The research findings demonstrate the significant presence of eucalypt in natural protected areas and the possibility of expansion of eucalypts in Galicia in the absence of effective control.

Keywords

Tasmanian blue gum, species distribution model, potential expansion, natural protected areas, environmental variables, Random Forest, Climate Change.

1. Introduction

Trees of the genus *Eucalyptus* were introduced to Europe at the end of the 18th century for ornamental purposes (Jacobs, 1981; Silva-Pando and Pino-Pérez, 2016). The suitability of the genus in the ecological conditions of Southern Europe, its high growth rate and the potential uses for the wood led to eucalypts being planted in forest land and a gradual increase in plantations in the 19th century. However, the greatest expansion of eucalypt plantations (mainly *Eucalyptus globulus*) in Europe occurred from the middle of the 20th century and was mainly driven by the demand for wood pulp to produce paper (Bermudez et al., 2002; Alegria et al., 2020). Nowadays, eucalypt plantations in Southern Europe occupy an area of approximately 1.3 million hectares, mainly in the Iberian Peninsula (more than 80 %), France and Italy (Cerasoli et al., 2016). This area is four times larger than the corresponding area in 1970 (Deus et al., 2018).

Currently, *E. globulus* is the most widespread fast-growing species in Spain, and with the exception of southwest Spain, it mainly occurs in seaboard areas in four autonomous communities in northern Spain (Galicia, Asturias, Cantabria and Euskadi). According to the recent update of the fourth Spanish national forest inventory (SNFI 4.5), *E. globulus* occupies a total land area of 389033.57 ha in the four autonomous communities, which represents 10.95% of the total forest area across these regions (MAPA, 2019a). Together with maritime pine and radiata pine, eucalypts are the most important commercial tree species in terms of timber production. In the period 2005-2016, the average harvested volume of *E. globulus* reached 4900219.60 m^3/year, which represents 54.06% of the total volume harvested annually (TVHA) in the four autonomous communities and 33.69% of the TVHA in the whole of Spain (MAPA, 2019b). Nevertheless, there are large differences between the autonomous communities. Thus, *E. globulus* is of great commercial importance in Asturias and Cantabria (73.38% and 82.04% of the TVHA), of intermediate-high importance in Galicia (49.38% of TVHA) and of low importance in Euskadi (11.43% of TVHA) (MAPA, 2019b).

Planting *E. globulus* is very controversial in the study area. On the one hand, the high growth rate, with maximum annual increments in volume up to 32‒36 m^{3}/ha$^{/}$year in the best sites (García-Villabrille, 2015; Viera et al., 2016), and profitability have led to the species being strongly promoted by some owners and pulp companies. In addition, the plantations create employment and wealth in rural areas and are very efficient as atmospheric CO_2 sinks (e.g. Castaño-Santamaría et al., 2013; Gómez-García, 2020). On the other hand, the practice of planting eucalypts has been strongly criticized by conservationists because of the potential ecological impacts. Different studies have analyzed the effects of these plantations on biodiversity, soils and hydrological responses (e.g. Poore and Fries, 1985; Calvo de Anta, 1992; Castro-Díez et. al., 2012; Bayle, 2019; Goded et al., 2019). Nevertheless, the controversy surrounding some negative impacts remains unsolved because it is context dependent (Deus et al., 2018).

The high profitability of commercial plantations of *E. globulus* has led some forest owners to clear-cut patches of native forest for reforestation with eucalypts. This land use change is forbidden by forest laws in the above-mentioned four autonomous communities in northern Spain, but is inadequately monitored and does occur. The substitution of native forests by eucalypt plantations is associated with two major environmental impacts (Montero de Burgos, 1990; Veiras and Soto, 2011): *i*) removal of stands that are much more diverse than eucalypt plantations and that can act as corridors connecting areas of high diversity; and *ii*) the eventual creation of large, continuous eucalypts plantations, which can exacerbate the negative impacts.

Eucalyptus globulus is very flexible in regard to climate and soil characteristics (e.g. Jacobs, 1981; Whitehead and Beadle, 2004). The most suitable areas for the species are characterized by mild and temperate climates with annual rainfall greater than 400‒500 mm with dry season up to three months, but not severe drought, as this species is highly sensitive to drought (Jacobs, 1981; Whitehead and Beadle, 2004). Although the expansion of *E. globulus* plantations around the world has inevitably increased the range of site conditions encountered, in relation to precipitation and temperature, most plantations have been established in regions with annual rainfall higher than 500–600 mm and mean annual temperature of 14±4 ºC (e.g., Pohjonen and Pukkala, 1990; Geldres and Schlater, 2004; Wang and Baker, 2007; Harper et al., 2009; Cerasoli et al., 2016; Alegria et al., 2020). The areas planted are not prone to frost, as low temperature is one of the main constraints to the presence of the species, and minimum temperatures below -5 ºC cause up to 50% of foliar tissue mortality (Almeida et al., 1994).

On the other hand, climate change is already a global phenomenon driven by rising levels of greenhouse gases in the atmosphere (IPCC, 2013). Increased atmospheric concentrations of CO_2 and other greenhouse gases will affect the growth and survival of plants species as well as their abundance and geographical distribution through changes in climate (temperature and precipitation) as well as through changes in photosynthetic rates and water use efficiency (Booth, 2012). In fact, according to projections of the CMIP5 model of the Intergovernmental Panel on Climate Change, these geographical regions will undergo a gradual increase in mean annual temperature (of between 1.3 and 2.5 ºC) together with a decrease in annual precipitation (of between 68 and 142 mm). A changing climate may also increase the incidence of many of the threats to forests, such as pests and diseases, invasive species, wildfires, storms and drought (Dale et al., 2001)).

Quantitative analysis of the potentially suitable habitat for a particular species and the shifts expected under climate change is essential. This type of analysis is even more important within the framework of exotic species such as eucalypts, for which the current or future potential suitable habitat may already be covered by native broadleaved forests or fall within natural protected areas (NPAs). The models used to predict this suitable habitat (region where the species occurs or potentially occurs) on the basis of environmental variables are known as Species Distribution Models, SDMs (Guisan and Zimmermann 2000; Booth et al., 2014). As a consequence of using climate variables as predictors, SDMs were initially considered an appropriate tool for predicting species suitable habitat under uncertain climate projections. Thus, SDMs were first used in climate change studies of both native forest and plantations in 1988 and have been widely used since then (Booth et al., 2014). On other hand, species distribution modelling has been criticized for only using abiotic variables and omitting other important exploratory variables such as biotic interactions, regeneration limitations and adaptive capacity (e.g. Pearson and Dawson, 2003; Sinclair et al., 2010). However, in the present study many of these limitations are not important, because we are dealing with a planted species whose distribution is not dependent on its natural dispersal ability and because cultivation operations usually reduce negative competition interactions with other species (Deus et al., 2018) and promote positive interactions.

A variety of statistical approaches ranging from multiple linear regression to complex machine learning algorithms have been used to predict species occurrence (e.g. Casalegno et al., 2011; Falk and Hempelmann, 2013; Roces-Díaz et al., 2015; Serra-Varela et al., 2017; Shirk et al., 2018; Castaño-Santamaría et al., 2019). As simulating changes in species cover in relation to environmental variables can be an extremely complex process, this poses significant challenges to traditional parametric regression analysis, so that non-parametric methods have become more popular (Prasad et al., 2006).

The main goals of the present study were to analyze the current cover of *E. globulus* in northern Spain and to develop a raster-based distribution model to predict the current and future suitable habitat for the species within the framework of climate change. The following specific objectives were established: *i*) to determine the current presence of *E. globulus* in the whole study area and within NPAs; *ii*) to investigate the environmental factors determining the current suitable habitat; *iii*) to develop an SDM and derive a spatially-continuous map of suitable habitat based on current environmental variables; *iv*) to make future projections of the model and map based on different climate change scenarios; and *v*) to examine the overlap between the current and future suitable habitat for *E. globulus* over native forest and other natural and seminatural areas and NPAs under climate change.

2. Materials and methods

2.1. Study area

The study area covers four autonomous communities in northern Spain: Galicia, Asturias, Cantabria and Euskadi (40.6° to 45.0° N; -9.6° to -1.5° W) (Fig. 1). Plantations of *E. globulus* are mainly established in the Eurosiberian biogeographical region within these communities. This biogeographical region extends along the seaboard of northern Spain, with the main axis running in an east-west direction, from the Galician Atlantic coast to the western extreme of the Pyrenees in Euskadi. The landscape of the area is complex, and the different combinations of topographic variables and landform strongly influence the type and vigour of the vegetation communities. The climate is generally characterized by mild temperatures (average annual values between 11.5 ºC and 14.5 ºC) and precipitation that is quite uniformly distributed throughout the year, often greater than 1000 mm per year (Nicolás and Iglesias, 2012). Geologically, ancient Palaeozoic rocks (carboniferous limestone, slate, coal, conglomerates, quartzite and sandstone) predominate in the central axis, flanked by Mesozoic (limestone, dolomite and sandstone) and Tertiary rocks in the lower mountains of the eastern part of the Basque Country (IGME, 2015a).

Insert here Figure 1 (print in color)

2.2. Data sources and preprocessing

Five different types of data were considered in this study and used for different purposes: *i*) *E. globulus* point occurrence data were used to develop the species distribution model; *ii*) data on current spatial environmental variables were used to model and map species distribution; *iii*) future climatic data projections under different emission scenarios were used to predict the impact of climate change on species distribution; *iv*) land use spatial information was used to assess changes in eucalypt cover and the potential effects on native forests and other natural and seminatural areas; and *v*) the spatial limits of the Spanish NPAs were used to assess the potential impact of eucalypt presence in these areas.

2.2.1 Occurrence data

Information on eucalypt occurrence was drawn from the plots of the Third Spanish National Forest Inventory (SNFI3). The plots are located at the nodes of a 1 km UTM square grid, comprising four concentric subplots of radius of 5, 10, 15 and 25 m, with a minimum diameter at 1.3 m above ground level threshold of 75, 125, 225 and 425 mm, respectively (MARM, 2006). This systematic grid of plots prevents omission of significant areas suitable for occupancy of the species. In total, 12773 plots within the study area were available for analysis and were imported to a GIS database (ArcGIS 9.3, ESRI, Redlands, CA, USA); *E. globulus* was present in 3014 of those plots. Presence was defined as the occurrence of one or more live eucalypt trees in each plot, and the plots were consequently classified as with or without eucalypt presence.

It is important to highlight that this inventory does not differentiate other species closely related to *E. globulus*, such as *Eucalyptus nitens* (currently commercially important). However, at the time of this inventory (which began in 1997 in Galicia and later in the other regions), the presence of *E. nitens* was not significant as commercial plantations of this species were first established in Galicia in 1992 (Perez-Cruzado, 2011).

2.2.2. Spatial environmental variables

Three types of environmental variables were considered as potential predictors of the species distribution model: terrain, climate and soil variables. A total set of 53 variables was finally used for analysis (Table 1).

Terrain variables were obtained from the 25 m resolution digital elevation model (DEM) provided by the Spanish National Plan for Aerial Orthophotography (PNOA; www.pnoa.ign.es), by using SAGA software v.3.0.0 (Conrad et al., 2015). Seven topographic variables, three potential incoming solar radiation variables and one variable related to the distance from hydrographic networks were considered. Elevation was excluded from the analysis because it is strongly correlated with climatic variables such as temperature and precipitation. A total of 19 climate variables, mostly created in 1996 for the BIOCLIM package (Booth et al., 2014), were obtained with a 30 arc-second resolution (approximately 800 m) from WorldClim (Hijmans et al., 2005). Twenty-five soil variables were also considered. Twelve variables (related to both physical and chemical soil properties) were compiled from the SoilGrids250m (Hengl et al., 2017). Five variables (chemical properties) were obtained from raster maps with 500 m spatial resolution, produced by Ballabio et al. (2016) using the LUCAS 2009 TOPSOIL database belonging to the European Soil Data Center (ESDAC) (Panagos et al., 2012). Soil type and group were compiled from the European soil database (ESDB) v2.0. Lithostratigraphic type and permeability were obtained from the Spanish Stratigraphic Map (SSM) scale 1:200000, and geology and lithology groups were obtained from the Spanish Geological Map (SGM) scale 1:1000000 (IGME, 2015a; 2015b).

Raster grids of all terrain, climate and soil variables were subsequently resampled at 250 m resolution.

Insert here Table 1

2.2.3. Future climate data projections

Climate data projections are required in order to predict future suitable habitat under different climate change scenarios. We used the Global Climate Models for the 2050 and 2070 time horizons based on the CMIP5 model from the Intergovernmental Panel on Climate Change (IPCC) 5th assessment report (https://www.wcrp-climate.org/wgcm-cmip/wgcm-cmip5). Bioclimatic predictions for two contrasting representative concentration pathway (RCP) scenarios were considered. The first “moderate” scenario (RCP 4.5) assumes a CO_2

concentration of 650 ppm and a temperature increase of 1.0–2.6 °C by 2100; the second "pessimistic" scenario (RCP 8.5) considers a CO_2 concentration of 1,350 ppm and a temperature increase of 2.6–4.8°C by 2100 (van Vuuren *et al.* 2011; IPCC, 2013; Harris *et al.* 2014; Dyderski *et al.* 2017). Data were downloaded at the same spatial resolution as the current climate variables (30 arc-second) and were also subsequently resampled at 250 m resolution.

2.2.4. Assessing changes in the area occupied by eucalypts, land cover layers and natural protected areas

To assess the change in *E. globulus* cover in the last few decades, data from the first four Spanish national forest inventories (SNFI1, SNFI2, SNFI3 and SNFI4) were used (MARM, 1966; 1986; 2006; 2012). The current eucalypt distribution was obtained from the recent update of SNFI4, carried out only for the most productive forest species in northern Spain, hereinafter referred to as SNFI4.5. In combination with this inventory, a vectorial forest-cover map was constructed (scale 1:25000) and updated in 2018 (MAPA, 2019a). This map provides an accurate delineation of eucalypt-dominated forest, with an optimum pixel size of 10-15 m and a minimum mapping area ranging from 0.5 to 2 ha.

To assess the types of land cover and land use that could be affected by a hypothetical expansion of eucalypt in suitable habitat, we used the 2018 version of the CORINE Land Cover (CLC) database (CLC 2018) for Spain (EEA, 2019). This version of CLC is the first to use full coverage of Sentinel-2 imagery and provides the land-related data at 20 m spatial resolution and considering a minimum mapping unit of 25 hectares (EEA, 2019). The nomenclature of the vector data has 3 hierarchical levels. The classes in the first level are artificial surfaces, agricultural areas, forests and semi-natural areas, wetlands and water. The second level has 15 classes and the third level, 44 sub-classes. Although the more detailed classes do not discriminate tree species, use of this database enabled us to differentiate different types of forest cover (coniferous, broadleaved and mixed forest) and other land use types.

To analyze the surface area covered by eucalypts and the distribution of land cover types in NPAs, we used the official, freely available vectorial data for these areas (MITECO, 2019)

2.3. Species distribution model

2.3.1. Modelling framework and model fitting

The distribution of eucalypts in northern Spain is a result of a human-induced expansion during more than 100 years. Considering the large surface area currently covered by the species, it is reasonable to assume that it currently occupies suitable habitat for growth, and that we therefore have reliable information for fitting a species distribution model. With this aim, eight different machine learning algorithms, namely Artificial Neural Networks (ANNs), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Boosted Models (GBMs), General Linear Models (GLMs), Maximum Entropy modelling (MAXEnt), Random Forest (RF) and rectilinear Surface Range Envelop (SRE), were tested. For this purpose, we used the freely available BIOMOD2 R software (Thuiller et al., 2016). Once the best algorithm was selected, it was fitted with the BIOMOD software for further assessment, evaluation and implementation. To select the potentially most important regressor variables, a wrapper methodology was used to select the subsample of variables, as this usually produces the best results (Zhiwei and Xinghua 2010) in terms of maximization of the area under the ROC curve.

2.3.2. Model assessment and analysis

The 10-fold cross-validation approach was used to test the accuracy of the algorithms. This process consists of four steps. In the first step, the data set is split into 10 random subsets each of roughly the same size. The model is then fitted 10 times, sequentially omitting one of the subsets each time. Each of the fitted models is then used to produce pseudo-independent predictions on the omitted subset, providing a good indication of how well the classifier will perform on unseen data. Finally, a confusion matrix that reflects the four possible ways that a sample point can be classified was used to calculate several commonly used metrics (Shirk et al., 2018): *i*) the overall accuracy, *ii*) the true skill statistic, *iii*) Cohen's kappa; and *iv*) the area under the ROC curve. The algorithm reports a probability of presence (PoP) of eucalypts as an output variable. A binary output is needed to calculate Cohen's Kappa and overall accuracy, and therefore a threshold PoP was selected to convert PoP to binary presence–absence outputs. To select this threshold ($PoP_{threshold}$), we used the average value of the PoP that maximized the sum of sensitivity (true positive rate) and specificity (true negative rate) and the PoP that minimized the difference between the absolute values of sensitivity and specificity.

For implementation, machine learning algorithms have an embedded feature ranking technique called the variable importance measure (VIM), used in the present study to determine the importance or "weight" of each variable in the model. To ensure that values of variable importance were expressed on comparable scales, the VIM values were normalized so that their sum was a unitary value (normalized importance), and they were also expressed in relative terms (relative importance = $(VIM-VIM_{min})/(VIM_{max}-VIM_{min})$). Marginal response curves were then constructed to enable exploration of the relationships between the response and each of important predictor variables. These curves represent the predicted PoP of the species prediction value (*y-axis*) as a function of a single environmental variable (*x-axis*), when all other explanatory variables were held constant at their mean values.

2.4. Predicting suitable habitat for eucalypt from land cover types

Once the best model was selected, it was applied to the current environmental spatial variables resampled to a 250 m × 250 m resolution to generate a spatially continuous map of current suitable habitat. In addition, the model was applied to the future climate variables reflecting two climate change scenarios, i.e. moderate (RCP 4.5) and pessimistic (RCP 8.5) for two time horizons (2050 and 2070).

In order to quantify the current surface area of the different types of forest and semi-natural land located in the predicted suitable habitat for *E. globulus*, the following four layers were superimposed: *i*) current or future suitable habitat obtained in the present study; *ii*) current cover by broadleaved forest (code 311 of CLC2018); *iii*) current cover by other forest and semi-natural land (CLC2018); and *iv*) current *E. globulus* cover ($EUGL_{SNFI4.5}$) obtained from the SNFI4.5.

The current surface area occupied by broadleaved forests within the potential habitat for eucalypt that does not overlap with current eucalypt cover was catalogued as native broadleaved forest. This assumption is valid as the recent SNFI4.5 has only inventoried 1,217.6 ha of exotic broadleaved forests (*Acacia* sp.) within the *E. globulus* suitable habitat in the whole study area.

As result of this procedure, the following five suitable habitats categories were examined in further detail:

- Suitable habitat in areas of native broadleaved species (SH_{NBF}): surface area for potential expansion of eucalypt in current native broadleaved forests (code 311 of CLC2018) minus the current area occupied by eucalypt ($EU_{SNFI4.5}$) and acacia stands.
- Suitable habitat in other natural and semi-natural areas (SH_{FSA}): surface area for potential expansion of eucalypt on forest land not catalogued as broadleaved forest. Specifically, the habitat comprises the following CLC2018 codes: 312 (coniferous forest), 313 (mixed forest), 321 (natural grassland), 322 (moor and heathland), 323 (sclerophyllous vegetation), 324 (transitional woodland-shrub), 333 (sparsely vegetated areas) and 334 (burnt areas).
- Net suitable habitat (SH_{NET}): total surface area occupied by forest and semi-natural land included in suitable habitat. This is the sum of $SH_{NBF,}$ SH_{FSA} and $EU_{SNFI4.5}$.

- Suitable habitat in non-forest land (SH_{NFL}): surface area of suitable habitat in terrain classified as non-forest land (artificial surfaces, agricultural areas, wetlands and water bodies) according to CLC2018.
- Gross suitable habitat (SH_{GROSS}): total surface area of suitable habitat. This is the sum of SH_{NFL} and SH_{NET}.

To quantify the distribution of potential suitable habitat for eucalypt over the land cover classes in protected areas, we superimposed the vectorial maps of NPA on the eucalypt-suitable habitat using GIS software.

2.5 Metrics of the different land cover types

Analysis of the dynamics and patterns of vegetation patches is very important for biodiversity conservation as these parameters are usually strongly correlated with various different ecological processes (Wang et al., 2014). In the present study, this analysis was carried out using data on the current habitat of *E. globulus*, native broadleaved and other forest types and also over the future suitable habitat projections for eucalypts under two different climate change scenarios.

The FRAGSTATS 4.2 spatial analysis program (McGarigal *et al.*, 2016) was used to quantify the degree of habitat fragmentation based on a binary model. Three indicators were used to quantify the surface area of suitable habitat: *i*) total area, *ii*) mean patch area and *iii*) largest patch index (the proportion of the landscape encompassed by the largest patch). The fragmentation was assessed using the aggregation index, which equals 0 when suitable habitat is maximally disaggregated into single grid cell patches disconnected from all other patches and increases to 1 as suitable habitat is increasingly aggregated into a single, compact patch. The degree of change was also quantified for each future scenario relative to the current situation, classifying habitat as either gained, maintained or lost.

3. Results

3.1. Species Distribution Model

Of the 12773 sites surveyed in the four autonomous communities in northern Spain, eucalypt was present at 3014 sites and absent from 9759 sites. Eucalypt was present at elevations ranging from 0 m to 785 m (mean elevation = 229 m), and the latitudinal distribution among the sampled sites ranged from 41.87 to 43.76 degrees north (mean latitude = 43.09 degrees north).

After comparing eight modelling techniques (Table 2), we selected the non-parametric RF ensemble learning method as the best approach for fitting SDMs and therefore for predicting the suitable habitat for the species. The selected model performed very well, with an overall accuracy of 0.87 and an area under ROC curve (AUC) of 0.93 (Table 2). As result of the feature selection process, 18 of the 53 variables were retained as the optimal subset size, indicating that suitable habitat of the species is driven by many interrelated variables with no clear predominance of any of them (Table 3). According to the normalized importance scores, the climate variables contributed most (45.87%) to the predictive capacity of the model, with thermal variables making a greater contribution than pluviometry variables (28.45% and 17.42%, respectively). Eight soil variables were retained and contributed 34.24% to the model. Most of these variables were related to chemical properties (21.41% of contribution), whereas the physical properties only contributed 9.31%. Three terrain variables contributed 14.89% to the model but all were variables with low relative importance, except for potential radiation at the equinox.

Insert here Table 2 and Table 3

The functional form of the marginal response plots for the eight most important variables (accumulated normalized importance of 50%) was unimodal or multimodal (Fig. 2), with different trends in the observed probability of presence (PoP). Isothermality (BIO03) had a maximum response in PoP between 37% and 42%; the response of maximum temperature in the warmest month (August) produced a peaked at around 23 ºC and rapidly diminished up to 28 ºC; the temperature seasonality (BIO04) produced a peak of PoP at temperature seasonality of 350% and a later rapid decreased up to 500%; for the mean temperature of the wettest quarter (BIO8) the maximum PoP response occurred at around 9-10 °C; for the precipitation of the wettest month (BIO13) the peak PoP was reached at 250 mm; the potential solar radiation in the equinox presented a peak of PoP at around 3250 kJ m^2 $year^{-1}$; precipitation in the wettest quarter (winter) (BIO16) had a PoP of 50% or greater with precipitation above than 320 mm; the cation exchange capacity of soils reached a maximum PoP around 22 cmol+ kg^{-1} and decreased at higher values.

Insert here Figure 2

3.2. Changes in surface area up to 2018 and current surface in natural protected areas

The surface area occupied by eucalypt has increased 4.6-fold in the last 50 years (from 84323 ha in 1966-1974 to 389025 ha in 2018). Nevertheless, analysis of the change in the four autonomous communities revealed some differences. Thus, the surface area occupied by eucalypts has increased 11.29-fold in Galicia, 1.90-fold in Asturias, 1.20-fold in Cantabria and 6.99-fold in the Euskadi (Table 4). The current cover by eucalypts in northern Spain represents on average 18.22% of the wooded area in the four autonomous communities. Again, analysis of the data for the four autonomous communities revealed significant differences. Thus, this species represents only 2.69% of the wooded area in Euskadi, 15.46% in Asturias, 19.47% in Cantabria and 23.82% in Galicia. Considering the data for the different provinces of the region where *E. globulus* occupies the largest surface area (Galicia), we found some very important differences: i) in the inland province of Ourense, *E. globulus* only represented 0.28% of the wooded area, ii) by contrast, in A Coruña 44.76% of the wooded area is covered by eucalypt stands (Table 4). The recently updated NFI (SNFI4.5) is the first to distinguish between the two eucalypt species, detecting 64817.79 ha cover by *E. nitens* in the study regions (mainly in Galicia, with 58156.06 ha), with the proportion of the wooded area occupied by eucalypt plantations increasing up 21.25% overall and up to 53.66% in A Coruña (Table 4).

The surface area occupied by *E. globulus* in NPA reached 7840.40 ha in the four autonomous communities, representing only 2.02% of the total area occupied by the species. Nevertheless, important differences were observed between the provinces (Table 5).

The fragmentation analysis of the current surface occupied by eucalypt ($EUGL_{SNFI4.5}$) and broadleaved forests (SH_{NBF}) revealed differences between provinces. Thus, the highest mean patch area (MPA) for eucalypt reached 23.79 ha in A Coruña and 51.54 ha in Lugo, and decreased to 3.38 ha in Ourense and 1.85 ha in Guipuzcoa. Conversely, the values for native broadleaved forests were lowest in the former provinces (5.25 and 4.52 ha, respectively) and highest in the latter provinces (16.90 and 11.78 ha, respectively). The contrasting values of this metric are also supported by the Aggregation Index (AI), which ranged from 90.35% in A Coruña to 93.33% in Lugo to 81.89% in Ourense and 80.00% in Guipuzcoa (Table S1).

Insert here Tables 4 and 5

3.3. Predicted effects of climate change on suitable habitat

SDM projections under two different future scenarios of emissions of greenhouse gases reveal an increase in the net suitable habitat (SH_{NET}). This increase varied between 14.16% and 22.36% by 2050 and between 17.82% and 34.14% by 2070, for the moderate and pessimistic climate change scenarios respectively. Despite the overall increase, clear differences between Galicia and the remaining three autonomous communities were observed according to the impact of climate change on SH_{NET}. In the western region of Galicia, large increases in SH_{NET} of 29.63% and 40.05% are expected by 2050 in the RCP 4.5 and RCP 8.5, respectively (Table 6, Fig. 3). Additional increases of 4.60% for RCP 4.5 and 6.11% for RCP 8.5 are also expected by 2070. The worsening climate change scenario (RCP 4.5 to RCP 8.5) has a greater impact (around 37% higher) on the increase in surface SH_{NET} than the predicted increase between 2050 and 2070. This increase occurs in the inland areas of eastern provinces of Lugo and Ourense. The other two provinces (A Coruña and Pontevedra) are currently almost totally suitable for eucalypt and will continue to be so in the both projected future climate change scenarios (Fig. 3).

In contrast to Galicia, a large reduction in SH_{NET} is expected for the other three autonomous communities (Table 6, Fig. 3) under the moderate climate change scenario. Thus, reductions of respectively 16.13% and 12.56% are expected for Asturias, 23.08 and 26.06% for Cantabria and 62.59 and 63.55% for Euskadi, for the temporal horizon of 2050 and 2070, respectively. The pessimistic scenario is expected to cause a greater reduction for the SH_{NET} reduction for Asturias and Cantabria (reductions of 23.22–11.33% and 33.33–13.18%) but a surprising contrasting effect in Euskadi for which loss in suitable habitat of 3.74% and gain of 85.79% are predicted for 2050 and 2070 time horizons, respectively (Table 6, Fig. 3).

Insert here Figure 3 (print in color)

3.4. Current and future potential expansion

The current surface area of suitable habitat for eucalypt available on forest land (SH_{NET}) is 1203756.11 ha, but an area of 372870.70 ha is already covered by this species (Table 6). Thus, the current SH_{NET} for eucalypt expansion is 830885.41 ha, representing a further 222.83% of current area that could be occupied by eucalypt plantations. Of this habitat, a total of 587448.01 ha is in Galicia, 148196.33 ha is in Asturias, 49923.33 ha is in Cantabria and 45317.75 ha to Euskadi. The SH_{NET} can be distributed in areas where native broadleaved forests and coniferous, mixed forest and non-wooded forest land currently occur (SH_{NBF} and SH_{FSA}, respectively (Table 6).

At present, 296356.71 ha of the suitable habitat for eucalypt is occupied by broadleaved native forest (Table 6, Fig. 4), some 185420.12 ha of which is in Galicia. Future projections indicate an increase in this suitable habitat up to 414705.96 ha by 2070 under the worst climate change scenario (RCP 8.5), most of which is also located in Galicia (307473.67 ha).

Insert here Table 6 and Figure 4 (print in color)

3.5. Current and future suitable habitat on natural protected areas

The current situation and future suitable habitat for eucalypt in NPAs varies substantially between the different autonomous communities. Currently, in Galicia, eucalypts occupy 5032.65 ha in NPAs. However, the current suitable habitat for *E. globulus* in these areas is more than 67800 ha. Under moderate (RCP 4.5) and pessimistic (RCP 8.5) climate change scenarios, this area is expected to increase to more than 107900 ha and 122400 ha respectively by 2070 (Table 5).

In the remaining autonomous communities, the area of *E. globulus* suitable habitat in NPAs is currently 42592.14 ha, but the area currently occupied by this species in NPAs is 2807.75 ha. In contrast to Galicia, a reduction in suitable habitat in the NPAs in these communities (of between 18.41% and 30.59%) is expected, except for the 2070 time horizon and under the worst scenario, for which an increase of 9.90% is expected.

4. Discussion

4.1. Species Distribution Model

Random forest was selected as the best technique for modelling suitable habitat for eucalypt in northern Spain. This is a widely used non-parametric classification approach that consists of constructing numerous decision trees from randomized subsets of predicted and predictor variables (Breiman, 2001). The success of the technique is based on the use of numerous trees, developed with different independent variables that are randomly selected from the complete original set of features (e.g. Deschamps et al., 2012; Wang et al., 2016). It has thus been recommended for ecological and species distribution modelling applications (Prasad et al., 2006; Araujo and Luoto, 2007). Moreover, it has also proved to be the best technique in some types of comparative analysis within the framework of species distribution modelling (e.g. Serra-Varela et al., 2017; Barrio-Anta et al., 2020) and has also been selected for modelling and mapping the suitability of European forest formations as a function of environmental factors (Casalegno et. al., 2011).

Concerning the importance of the predictor variables in the selected model, our findings showed that temperature-related variables are the environmental features with the strongest effects on the distribution of eucalypts in northern Spain. The probability of presence of the species is highest in areas where the variability in temperature (expressed by variables BIO03 and BIO04) is low, in accordance with the autoecological data for the species (Cerasoli et al., 2016). The former variable can be interpreted as a quantification of the day-to-night temperature oscillation relative to the summer-to-winter oscillation, whereas the latter is a measure of temperature change over the course of the year. This finding is consistent with recent findings on the autecology of this species in the whole of the Iberian Peninsula (Deus et al., 2018) and Portugal (Alegria et al., 2020), which showed that thermal variables were more important than pluviometric variables. In fact, the third most important variable in the present study, temperature seasonality, was the second most important in the aforementioned two studies.

The negative effect of the temperature in the warmest month (BIO05) on the probability of presence may be due to the negative correlation between temperature and growth during summer months (Downes et al., 1999), which in turn can be attributed to the higher respiratory costs of the highest temperatures (Battaglia and Sands, 1997).

The fifth and seventh most important variables are related to the precipitation in the wettest month (December) and in the wettest quarter (winter), which produced the highest PoP values of more than 115 and 325 mm, respectively. In its natural area of distribution, *E. globulus* usually occurs in areas with an annual rainfall of 600–1100 mm, and it is absent from areas with less than 500 mm of annual precipitation (Bean and Russo, 1989). A similar precipitation range was found for European plantations, although it can reach 1500 mm in some locations (Cerasoli et al., 2016). The high amount of precipitation in the study area (average annual value of 1132 mm) could justify the lower importance of pluviometry variables than of thermal variables. The fact that both the wettest month and the wettest quarter positive affected the PoP suggests that the level of water stored in the soil must have been adequate, resulting in slower depletion of soil water during summer.

The observed slightly negative trend in PoP with increasing cation exchange capacity could be mediated by soil texture or soil acidity. Soils with a higher proportion of clay or higher pH tend to have a higher cation exchange capacity. In a context of widespread abundance of precipitation, a high proportion of clay could lead to waterlogging, which can severely limit tree growth (Barton-Johnson, 2006; Viera et al., 2016). The absence of a clear influence of cation exchange capacity on PoP is consistent with the observed capacity of the species to grow even in poor soils in its natural range (Grove et al., 1996). Previous studies conducted in northern Spain (e.g. Brañas et al., 2000; Merino et al., 2003) have also concluded that the success of *E. globulus* in this area is partly due to its tolerance to acid soils and low P, Ca and Mg requirements.

Solar radiation may influence suitable habitat indirectly through variables such as temperature and soil moisture content.

4.2. Predicted effects of climate change on suitable habitat

Although a large area is currently occupied by eucalypts in northern Spain, according to the SDM developed, there is potential for the area to continue to increase. Thus, our SDM predicts a substantial expansion of the eucalypt-suitable habitat in Galicia (NW Spain) for both moderate and pessimistic climate change scenarios. By contrast, no change or a slight to moderate reduction is predicted for the other three autonomous communities (Asturias, Cantabria and Euskadi). Similar projections have been made by Deus et al. (2018) in a study of the whole Iberian Peninsula.

Retraction of suitable habitat in the three autonomous communities bordering the Cantabria Sea seems to be due to precipitation-related variables, and more specifically to the precipitation in the wettest quarter (BIO16). This variable has a peak of PoP around 325 mm with a rapid decrease at lower values (Fig. S1). The current maximum density for this variable is rather low (around 300 mm) and will decrease to around 275–280 mm in the future climate change scenarios. By contrast, although the maximum density of precipitation of the wettest quarter (BIO16) will probably decrease to 400–450 mm, from the current maximum of 475 mm, in Galicia, this will still be a greater amount of precipitation that presumably will have no effect on the suitable habitat. This possibility is also supported by analysis of the precipitation of the wettest month (BIO13), in which PoP increases with BIO13 values higher than 120 mm. In the other three autonomous communities, the maximum value of BIO13 is around 117 mm and will decrease until 110 mm under the expected climate change scenario, whereas for Galicia the current value is 175 mm and will decrease to 150–160 mm.

In summary, the substantial increase in *E. globulus* suitable habitat will occur in the inland provinces of Galicia (NW of the study area) and will be driven by the reduction in isothermality (BIO03). By contrast, the expected patterns of decrease in winter precipitation will probably reduce the *E. globulus* suitable habitat in the three seaboard autonomous communities under expected climate change (Fig.S2).

4.3. Changes in surface area, current surface cover and future potential expansion

After the initial establishment of commercial eucalypt plantations in around 1850 (Lama Gutierrez, 1976; Silva-Pando and Pino-Pérez, 2016), and similar as has been pointed out for Portugal (Alegria et al., 2020), the plantations rapidly expanded throughout Spain’s northern seaboard, mainly driven by economic factors. The remarkable plasticity of the species in relation to soil and climate facilitated its adaptation (Jacobs, 1981; Bean and Russo, 1989), so that there have not been any noticeable environmental restrictions to eucalypt survival and growth in the study area (Lama Gutierrez, 1976; Jacobs, 1981).

The rapid increase in the area occupied by *E. globulus* has been accompanied by an increase in biomass stock and carbon fixation. For example, in Galicia, the biomass stock of *E. globulus* increased by 5.8 times in the period 1972–2009 (Gómez-García, 2020). In fact, *E. globulus* stands currently represent the maximum aboveground carbon stocks in this autonomous community (Gómez-García, 2020).

Although forbidden by forestry regional laws, substitution of native forest by eucalypt plantations has frequently occurred (Fig. 5). The main reason for this substitution is the enormous difference in the growth rate and the rotation ages compared with most native broadleaved species. For example, the current mean rotation age of *E. globulus* in Galicia is 12–16 years (Viera et al., 2016), much lower than the 110–145 years required to maximize stem volume production in pedunculate oak (*Quercus robur* L.) stands (Gómez-García et al., 2015). In addition, the regional forest authorities have had available limited resources for carrying out effective control to prevent the establishment of eucalypt plantations after native broadleaved forests are clear-cut. To protect and enhance native forests, some autonomous communities, such as Galicia, have established a database of native broadleaved forests covering areas greater than 15 ha. Owners of these areas will be eligible for tax benefits and will be given priority for receiving public grants for sustainable management and conservation (DOG, 2020).

Although the future climatic conditions seem to favour expansion of the suitable area for eucalypt, this does not necessary imply the establishment of new plantations. Legislation by regional governments to control and regulate the species and the socioeconomic changes and market demands will play a very important role in limiting, reversing or even encouraging expansion of the species (Deus et al., 2018). New challenges have also arisen concerning the expansion of the *Eucalyptus* genus in northern Spain. Thus, in the last decade *E. nitens* has been planted in frost prone areas at elevations up to 900–1000 m, mainly in inland areas of Galicia. Moreover, *E. nitens* plantations are also replacing clear cut radiata pine plantations and existing *E. globulus* plantations in areas affected by *Gonipterus platensis* (> 350 m.a.s.l. and shallow soils) because *E. nitens* is less susceptible to this pest (Gonçalves et al., 2019). Therefore, this newly planted species is expected to greatly increase the suitable habitat for eucalypt in the study area.

Insert here Figure 5 (print in color)

4.4. Cover in natural protected areas (NPAs)

The current cover of eucalypt within NPAs in the four autonomous communities under study is 7840.40 ha, representing 2.02% of the total surface area occupied by eucalypts. Moreover, most of the eucalypt plantations in NPA were established prior to the designation of protected areas, as previously pointed out for the whole Iberian Peninsula (Deus et al., 2018). Currently, some NPAs have restrictive regulations that forbid establishment of eucalypt plantations by private owners, and some autonomous communities (including Galicia) have forbidden the establishment of new eucalypt plantations within sites included into the Natura 2000 network.

In this regard, a gradual reduction in the area covered by eucalypts and promotion of broadleaved native forests would enhance the connectivity between protected areas and favour landscape heterogeneity.

5. Conclusions

The area currently occupied by eucalypts in northern Spain has increased fivefold in the last fifty years. The species currently covers an area of 389033.57 ha, which represent 18.22% of the wooded area in the autonomous communities under study. However, in A Coruña, a seaboard province with no extensive mountainous terrain, already suffers excessive plantation development -with more of 44% of the wooded surface occupied by eucalypt. In addition, 2% of the area occupied by eucalypts occurs within natural protected areas. Using the random forest technique and currently available spatially-continuous environmental variables, we developed a raster-based SDM (of resolution 250 m) of suitable habitat for eucalypt plantations. Projecting the model to two different climate change scenarios enabled us to distinguish areas with an expected substantial increase from others with an estimated reduction in suitable habitat (Galicia and the other three autonomous communities, respectively). Within the current suitable habitat, we identified an area of 830885.41 ha of forest land suitable for potential expansion of eucalypt, with an area of 296356.71 ha corresponding to current native broadleaved forest. This large area that can still be potentially occupied by eucalypt should urge forest decision-makers to develop sustainable forest management plans to control further expansion of these plantations and to reduce the high pressure of eucalypt plantations on higher-biodiversity natural broad-leaved forests.

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8. Tables

Table 1. Environmental variables included as possible predictors in the distribution model

Type	Code	Description	Unit	Source
Terrain	SLP	Slope based on a digital elevation model	%	PNOA
	ASP	Aspect based on a digital elevation model	º	
	CU	Curvature		
	PLC	Plan curvature		
	PRC	Profile curvature		
	TSI	Terrain shape index		
	WI	Wetness index		
	SR_SS	Potential incoming solar radiation at summer solstice	kJ m^2 year^{-1}	
	SR_EQ	Potential incoming solar radiation at equinox	kJ m^2 year^{-1}	
	SR_WS	Potential incoming solar radiation at winter solstice	kJ m^2 year^{-1}	
	DHN	Euclidean distance to hydrographic network	meters	
Climate	BIO01	Annual mean temperature	mm	WorldClim
	BIO02	Mean diurnal range (Mean of monthly (max temp - min temp))	mm	
	BIO03	Isothermality (BIO02/ BIO07) (*100)	%	
	BIO04	Temperature seasonality (standard deviation *100)	ºC	
	BIO05	Max temperature of warmest month	ºC	
	BIO06	Min temperature of coldest month	ºC	
	BIO07	Temperature annual range (BIO05- BIO06)	ºC	
	BIO08	Mean temperature of wettest quarter	ºC	
	BIO09	Mean temperature of driest quarter	ºC	
	BIO10	Mean temperature of warmest quarter	ºC	
	BIO11	Mean temperature of coldest quarter	ºC	
	BIO12	Annual precipitation	mm	
	BIO13	Precipitation of wettest month	mm	
	BIO14	Precipitation of driest month (mm)	mm	
	BIO15	Precipitation seasonality (coef. of variation)	%	
	BIO16	Precipitation of wettest quarter	mm	
	BIO17	Precipitation of driest quarter	mm	
	BIO18	Precipitation of warmest quarter	mm	
	BIO19	Precipitation of coldest quarter	mm	
Soil	SC	Soil organic carbon content	Mg/ha	SoilGrids250m
	Ph_H$_2$O	Soil pH in H$_2$O solution		
	Ph_KCl	Soil pH in KCl solution		
	BD	Bulk density of fine earth fraction (< 2mm)	kg m^{-3}	
	CLAY	Percentage of clay in soil	Weight %	
	SAND	Percentage of sand in soil	Weight %	
	SILT	Percentage of silt in soil	Weight %	
	CF	Coarse fragments	Volumetric %	
	CEC	Cation exchange capacity	cmol+ kg^{-1}	
	DB	Absolute depth to bed rock	cm	
	DB200	Depth to bedrock (R horizon) to 200 cm	cm	
	R	Probability of occurrence of R horizon	%	
	CaCO3	Calcium carbonates (CaCO3)	g kg^{-1}	LUCAS 2009 TOPSOIL database
	CN	C:N ratio		
	K	Potassium (K)	mg kg^{-1}	
	N	Nitrogen (N)	g kg^{-1}	
	P	Phosphorus (P)	mg kg^{-1}	
	Geo_units	Geology units		SGM
	Geo_lit_units	Lithology units		
	LIT_dco	Lithostratigraphy		SSM
	LIT_per	Lithostratigraphy permeability		
	WRB-FULL	Full soil code of the soil typological units from the World Reference Base (WRB) for Soil Resources		ESDB
	WRB-LEV1	Soil reference group of the soil typological units from the WRB for Soil Resources		

Table 2. Values of the goodness-of-fit statistics (after 10-fold cross validation approach) from the different statistical techniques tested for fitting the species distribution model: ANNs (Artificial Neural Networks), CTA (Classification Tree Analysis), FDA (Flexible Discriminant Analysis), GBMs (Generalized Boosted Regression Models), GLMs (Generalized Linear Models), MAXENT (Maximum Entropy), RF (Random Forest), SRE (Rectilinear Surface Range Envelope). The values in brackets are the standard deviations for the 10 predictions.

	Statistical technique							
	ANN	**CTA**	**FDA**	**GBM**	**GLM**	**MAXENT**	**RF**	**SRE**
AUC	0.8875 (0.0166)	0.8895 (0.0131)	0.9113 (0.0104)	0.9225 (0.0087)	0.8950 (0.0097)	0.9204 (0.0074)	0.9331 (0.0071)	0.7146 (0.0258)
OA	0.8378 (0.0160)	0.8517 (0.0105)	0.8518 (0.0096)	0.8601 (0.0097)	0.8332 (0.0118)	0.8561 (0.0083)	0.8705 (0.0070)	0.7963 (0.0137)
TSS	0.7069 (0.0234)	0.6977 (0.0163)	0.7244 (0.0104)	0.7315 (0.0170)	0.7049 (0.0157)	0.7303 (0.0167)	0.7551 (0.0147)	0.4291 (0.0521)
Kappa	0.6046 (0.0294)	0.6196 (0.0234)	0.6194 (0.0211)	0.6342 (0.0225)	0.5936 (0.0256)	0.6315 (0.0198)	0.6640 (0.0197)	0.4315 (0.0451)

Goodness-of-fit statistics: AUC (area under the ROC curve), OA (overall accuracy), TSS (true skill statistic), Kappa (Cohen’s kappa). Model fitting was assessed on the training data used to fit the model as well as the withheld test data used for model evaluation. All values represent the mean 10-fold cross-validation.

Table 3. Variables included in the development of SDM, including the type of the variable and its normalized and relative importance.

Type	Variable	Normalized Importance	Relative Importance	Summarized values in the suitable habitat			
				Mean	**Max.**	**Min.**	**S.D.**
Climate	BIO03	7.88	100.00	393.20	450.00	350.00	16.61
Climate	BIO05	7.08	78.41	23.77	28.40	19.70	1.11
Climate	BIO04	7.02	76.89	431.40	555.90	308.50	56.67
Climate	BIO08	6.47	61.98	8.22	13.40	0.50	2.08
Climate	BIO13	6.09	51.66	141.20	273.00	62.00	34.10
Climate	SR_eq	5.90	46.54	3358.20	4677.50	883.20	372.86
Climate	BIO16	5.76	42.77	383.60	662.00	166.00	87.11
Soil	CEC	5.69	40.98	27.18	43.00	17.00	3.53
Climate	BIO17	5.57	37.66	148.30	258.00	73.00	33.41
Soil	SC	5.47	34.92	46.15	69.00	22.00	7.14
Soil	K	5.23	28.55	148.80	641.90	111.10	64.55
Soil	P	5.02	22.80	16.82	0.00	59.28	9.62
Soil	SAND	4.72	14.81	40.72	61.00	18.00	6.98
Terrain	PRC	4.62	12.07	0.01	0.66	-0.60	0.11
Soil	DB	4.59	11.22	1388.00	6439.00	813.00	235.32
Terrain	SLP	4.37	5.43	10.70	43.87	0.02	6.94
Soil[1]	WRB-LEV1	4.35	4.85	-	-	-	-
Soil[1]	LIT_per1	4.17	0.00	-	-	-	-

[1] Qualitative variable

Table 4. Changes in the surface area (in hectares) occupied by eucalypts between 1966 and 1974 and until present (2018), quantifying the current surface of eucalypt as percentage of the total wooded surface (CLCw) according to the Corine Land Cover 2018 classification (CLC2018).

PERIOD	**Code**	**Galicia**				**Asturias**	**Cantabria**				**TOTAL**
		Pontevedra	**A Coruña**	**Lugo**	**Ourense**	**Asturias**	**Cantabria**	**Álava**	**Vizcaya**	**Guipuzcoa**	
PAST	**EU$_{SNFI1}$ (1966-1974)**	8182.00	15371.00	4086.00	0.00	25507.00	29697.00	0.00	1480.00	0.00	84323.00
	EU$_{SNFI2}$ (1986-1996)	11085.32	27040.06	8367.91	0.00	32824.01	32824.01	0.00	7675.90	0.00	86993.20
	EU$_{SNFI3}$ (1997-2007)	73779.47	175206.07	70995.37	860.63	71836.20	42968.78	36.53	9384.53	243.08	445067.58
	EU$_{SNFI4}$ (2008-2018)	66887.09	214313.98	75190.05	565.09	69713.93	41184.96	147.02	9772.66	353.46	477774.78
CURRENT 2018	**EUGL$_{SNFI4.5}$**	50846.87	169907.92	65835.46	579.80	56559.41	34956.38	0.00	9936.61	411.11	389033.57
	EUNI$_{SNFI4.5}$	1693.34	33799.67	22562.81	100.24	410.80	212.31	700.69	5166.78	171.14	64817.79
	EU$_{SNFI4.5}$	52540.22	203707.60	88398.27	680.04	56970.21	35168.69	700.69	15103.39	582.26	453851.36
	CLCf	290255.40	501619.84	647208.56	547022.54	745239.67	350047.65	175504.48	155206.59	140951.52	3553056.25
	CLCw	193307.40	379619.21	426715.06	205980.97	365911.49	179568.91	136002.85	128965.95	119671.57	2135743.40
	EUGL$_{SNFI4.5}$%	26.30	44.76	15.43	0.28	15.46	19.47	0.00	7.70	0.34	18.22
	EU$_{SNFI4.5}$%	27.18	53.66	20.72	0.33	15.57	19.59	0.52	11.71	0.49	21.25

Variables from the National Forest Inventories: **EU$_{SNFIx}$**: total area occupied by eucalypt plantations according to the different Spanish National Forest Inventories, **EUGL$_{SNFI4.5}$**: total area occupied by *Eucalyptus globulus* according to the recent update of the Fourth Spanish National Forest Inventory for major productive species in northern Spain (SNFI4.5). **EUNI$_{SNFI4.5}$**: total area occupied by *Eucalyptus nitens* according to SNFI4.5. **EUGL$_{SNFI4.5}$%**: percentage of area covered by *E. globulus* relative to the total wooded area (CLCw). **EU$_{SNFI4.5}$%**: percentage area covered by eucalypt (*E. nitens* + *E. globulus*) relative to the wooded surface (CLCw).

Variables from the 2018 version of Corine Land Cover (CLC2018): **CLCf**: Total area in the province occupied by forest and semi-natural areas (CLC2018 codes: 311 broadleaved forest; 312 coniferous forest; 313 mixed forest; 321 natural grassland; 322 Moor and heathland; 323 sclerophyllous vegetation; 324 transitional woodland-shrub; 331 beaches, dunes, sands; 332 bare rocks; 333 sparsely vegetated areas; 334 burnt areas; glaciers and perpetual snow. **CLCw**: total area in the province occupied by forest (CLC2018 codes: 311 broadleaved forest; 312 coniferous forest; 313 mixed forest).

Table 5. Area (in hectares) currently occupied by eucalypt, area of suitable habitat for eucalypt within Natural Protected Areas (NPA) and future predictions for the 2050 and 2070 time horizons under two different climate change scenarios.

	Autonomous Community	**Galicia**				**Asturias**	**Cantabria**	**Euskadi**			**TOTAL**
	Province	**Pontevedra**	**A Coruña**	**Lugo**	**Ourense**	**Asturias**	**Cantabria**	**Álava**	**Vizcaya**	**Guipuzcoa**	
CURRENT (2018)	$\mathbf{EUGL}_{\mathbf{SNFI4.5}}$	50846.87	169907.92	65835.46	579.80	56559.41	34956.39	0.00	9936.61	411.11	389033.57
	$\mathbf{EUGL}_{\mathbf{NPA}}$	161.36	3278.32	1584.95	8.03	339.83	1149.07	0.00	1292.98	25.87	7840.40
	$\mathbf{EUGL}_{\mathbf{NPA}}\mathbf{\%}$	0.32	1.93	2.41	1.38	0.60	3.29	0.00	13.01	6.29	2.02
	$\mathbf{SH}_{\mathbf{NPA}}$	13861.50	39109.31	12350.36	2515.47	3184.82	22548.49	0.00	16833.57	25.27	110428.78
2050	$\mathbf{SH}_{\mathbf{NPA\_RCP4.5}}$	19885.80	43729.26	23904.17	7991.55	2781.71	21194.79	0.00	6042.79	66.61	125596.67
	$\mathbf{SH}_{\mathbf{NPA\_RCP8.5}}$	21419.26	44263.13	21879.08	39848.74	2714.69	20954.69	0.00	8939.65	2141.09	162160.32
2070	$\mathbf{SH}_{\mathbf{NPA\_RCP4.5}}$	20886.37	44097.12	24865.36	18116.89	2748.54	20576.75	0.00	6186.51	52.81	137530.35
	$\mathbf{SH}_{\mathbf{NPA\_RCP8.5}}$	21224.32	44381.78	29353.27	27489.42	3036.82	22454.79	0.00	17153.90	4164.14	169258.43

$\mathbf{EUGL}_{\mathbf{SNFI4.5}}$: current total area occupied by *E. globulus*. $\mathbf{EUGL}_{\mathbf{NPA}}$: area currently occupied by *E. globulus* in NPA.s $\mathbf{EUGL}_{\mathbf{NPA}}\mathbf{\%}$: current percentage of *E. globulus* in NPA relative to $\mathrm{EU}_{\mathrm{SNFI4.5}}$. $\mathbf{SH}_{\mathbf{NPA}}$: current area of *E. globulus*-suitable habitat in NPAs. $\mathbf{SH}_{\mathbf{NPA\_RCP4.5}}$: area of *E. globulus*-suitable habitat in NPAs under the RCP 4.5 scenario. $\mathbf{SH}_{\mathbf{NPA\_RCP8.5}}$: area of *E. globulus*-suitable habitat in NPAs under the RCP 8.5 scenario.

Table 6. Surface area (in hectares) occupied by different types of land cover included in the eucalypt suitable habitat according to the fitted Species Distribution Model and future projections under two different future climate scenarios (RCP 4.5 and RCP 8.5).

Scenario	**Code**	**Galicia**				**Asturias**	**Cantabria**	**Euskadi**			**TOTAL**
		Pontevedra	**A Coruña**	**Lugo**	**Ourense**	**Asturias**	**Cantabria**	**Álava**	**Vizcaya**	**Guipuzcoa**	
CURRENT 2018	**CLCf**	290255.40	501619.84	647208.56	547022.54	745239.67	350047.65	175504.48	155206.59	140951.52	3553056.25
	CLCw	193307.40	379619.21	426715.06	205980.97	365911.49	179568.91	136002.85	128965.95	119671.57	2135743.40
	SH$_{NBF}$	66033.67	82944.76	28762.99	7678.69	69179.70	27729.85	39.28	13562.98	424.78	296356.71
	SH$_{FSA}$	122349.13	220676.46	45383.78	13618.53	79016.63	22193.47	314.56	29962.30	1013.86	534528.71
	EUGL$_{SNFI4.5}$	48924.67	166240.57	61197.78	178.67	54583.73	33346.71	0.00	8385.58	12.99	372870.70
	SH$_{NET}$	237307.47	469861.79	135344.55	21475.89	202780.06	83270.04	353.83	51910.86	1451.64	1203756.11
2050 RCP 4.5	**SH$_{NBF}$**	75934.47	85142.69	71625.89	32164.76	55467.90	21831.20	0.64	5914.56	190.44	348272.54
	SH$_{FSA}$	148164.14	230040.25	124789.67	71970.08	62045.35	13391.43	23.65	8229.68	660.83	659315.08
	EUGL$_{SNFI4.5}$	49370.05	166988.06	63365.57	406.44	52563.59	28827.42	0.00	5073.06	0.91	366595.11
	SH$_{NET}$	273468.66	482171.00	259781.12	104541.28	170076.85	64050.05	24.29	19217.30	852.17	1374182.72
2050 RCP 8.5	**SH$_{NBF}$**	76879.11	85196.88	78378.18	50063.82	47421.02	18702.91	6.99	6491.68	9224.38	372364.96
	SH$_{FSA}$	152366.69	231476.21	137541.37	118100.49	58839.68	11569.02	185.53	19135.15	11433.12	740647.25
	EUGL$_{SNFI4.5}$	49381.23	167038.42	63101.89	475.25	49426.31	25245.67	0.00	5027.58	203.85	359900.20
	SH$_{NET}$	278627.03	483711.51	279021.44	168639.55	155687.01	55517.61	192.52	30654.41	20861.34	1472912.41
2070 RCP 4.5	**SH$_{NBF}$**	76091.32	85196.87	75266.38	37349.53	58050.45	20438.32	0.12	5172.33	340.52	357905.84
	SH$_{FSA}$	150154.42	231122.86	136828.63	87396.61	66375.73	12959.64	22.75	8687.78	690.60	694239.02
	EUGL$_{SNFI4.5}$	49372.69	167028.76	63490.44	444.43	52888.44	28171.77	0.00	4663.65	3.30	366063.50
	SH$_{NET}$	275618.43	483348.50	275585.45	125190.57	177314.63	61569.73	22.88	18523.76	1034.42	1418208.35
2070 RCP 8.5	**SH$_{NBF}$**	77429.48	85199.32	95532.17	49312.71	58368.12	24338.28	200.79	11197.87	13127.23	414705.96
	SH$_{FSA}$	153462.74	231665.75	176800.91	112913.90	71856.73	18951.42	2037.60	47034.20	18847.54	833570.77
	EUGL$_{SNFI4.5}$	49381.23	167052.99	63580.84	467.93	49576.33	29005.36	0.00	7090.82	263.51	366419.03
	SH$_{NET}$	280273.44	483918.06	335913.92	162694.54	179801.18	72295.06	2238.39	65322.89	32238.28	1614695.76

Variables from the updated Fourth National Forest Inventory (SNFI4.5): **EUGL$_{SNFI4.5}$**: area currently occupied by *E. globulus* plantations.

Variables from the 2018 version of Corine Land Cover (CLC2018): **CLCf**: total area in the province covered by forest and semi-natural areas (CLC2018, codes: 311 broadleaved forest; 312 coniferous forest; 313 mixed forest; 321 natural grassland; 322 moor and heathland; 323 sclerophyllous vegetation; 324 transitional woodland-shrub; 331 beaches, dunes, sands; 332 bare rock; 333 sparsely vegetated areas; 334 burnt areas; glaciers and perpetual snow. **CLCw**: total area in the province occupied by forest (CLC2018, codes: 311 broadleaved forest; 312 coniferous forest; 323 mixed forest).

Variables gathered across CLC2008, SNFI4.5 and SDM areas: **SH$_{NBF}$**: area of potential expansion of eucalypt in current native broadleaved forest (CLC2018 code 311 (Broadleaved forest) minus EUGL$_{SNFI4.5}$, minus EUNI$_{SNFI4.5}$ and minus surface of *Acacia* sp formations). **SH$_{FSA}$**: area of potential expansion in other natural and semi-natural areas. **SH$_{NET}$**: area of CLCf included in the suitable habitat, SH$_{NET}$ = EU$_{SNFI4.5}$ + SH$_{NBF}$ + SH$_{FSA}$.

Note: future projections for SH$_{NBF}$ and SH$_{FSA}$ were determined considering the projected future net suitable habitat (SH$_{NET}$) but considering the current CLCf and CLCw cover in order to assess the extent of the impact on the contemporary cover by native broadleaved forest or other types of forest.

9. Figure Captions

Figure 1. Location of the study area.

Figure 2. Marginal response curves for the seven most important variables included in the eucalypt species distribution model. The variables are presented in order of their contribution to the model (importance score). The black line indicates the mean and the grey shaded area the standard deviation of the probability presence (PoP).

Figure 3. Spatially explicit model predictions of current and future suitable habitat of *E. globulus* under two different climate change scenarios (RCP 4.5 and RCP 8.5) for the 2050 and 2070 time horizons.

Figure 4. Spatial distribution of land cover types within suitable habitat for *E. globulus*: current estimations and predictions for the 2050 and 2070 time horizons under two different climate change scenarios (RCP 4.5 and RCP 8.5).

Figure 5. Illustration of the replacement of a native forest by eucalypt plantations. Photograph from the municipality of As Somozas, Galicia (NW Spain) in the early 2000s. © M. Barrio-Anta.

10. Figures

Fig 1.

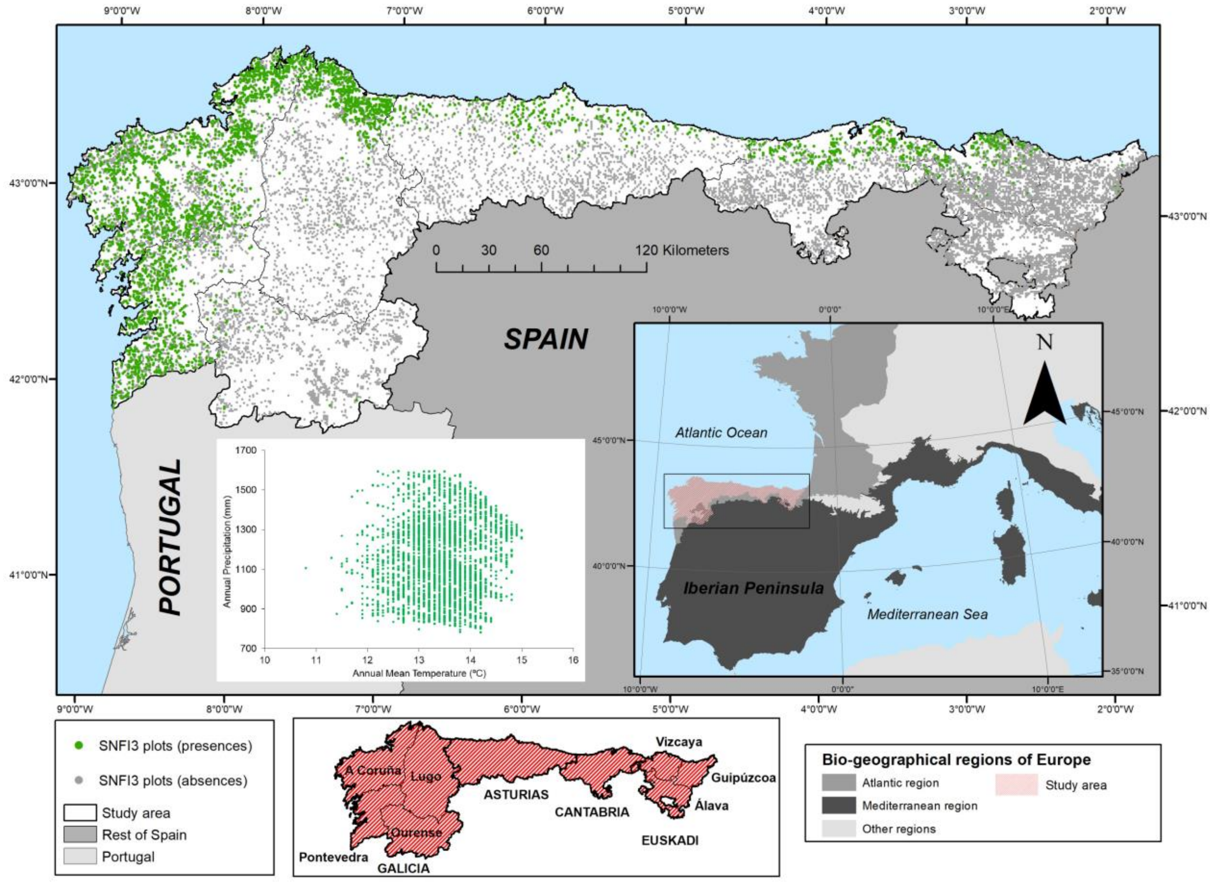


Fig 2.

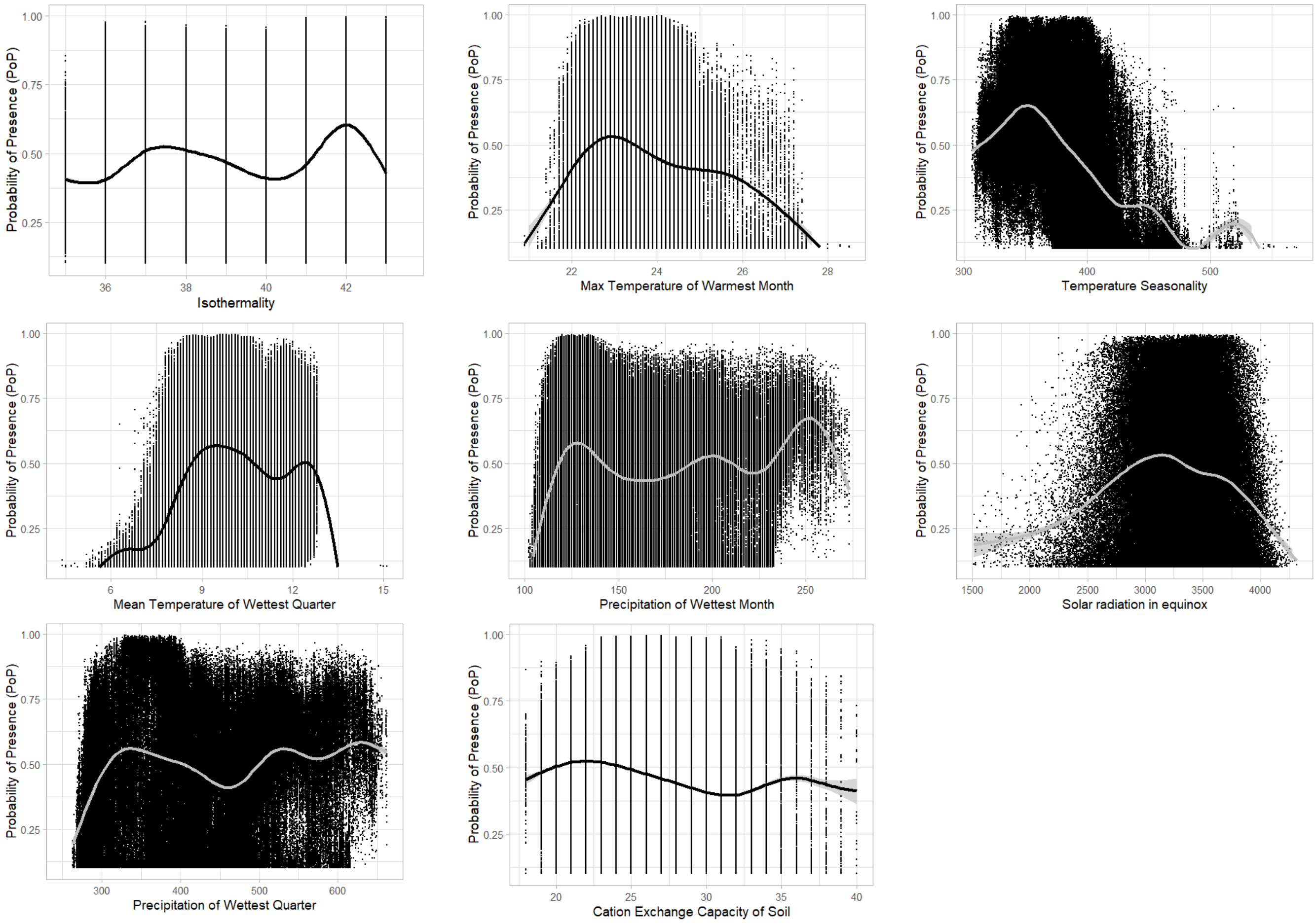

Probability of Presence (PoP)
0.25
0.50
0.75
1.00
36
38
40
42
Isothermality
22
24
26
28
Max Temperature of Warmest Month
300
400
500
Temperature Seasonality
6
9
12
15
Mean Temperature of Wettest Quarter
100
150
200
250
Precipitation of Wettest Month
1500
2000
2500
3000
3500
4000
Solar radiation in equinox
300
400
500
600
Precipitation of Wettest Quarter
20
25
30
35
40
Cation Exchange Capacity of Soil

Fig 3.

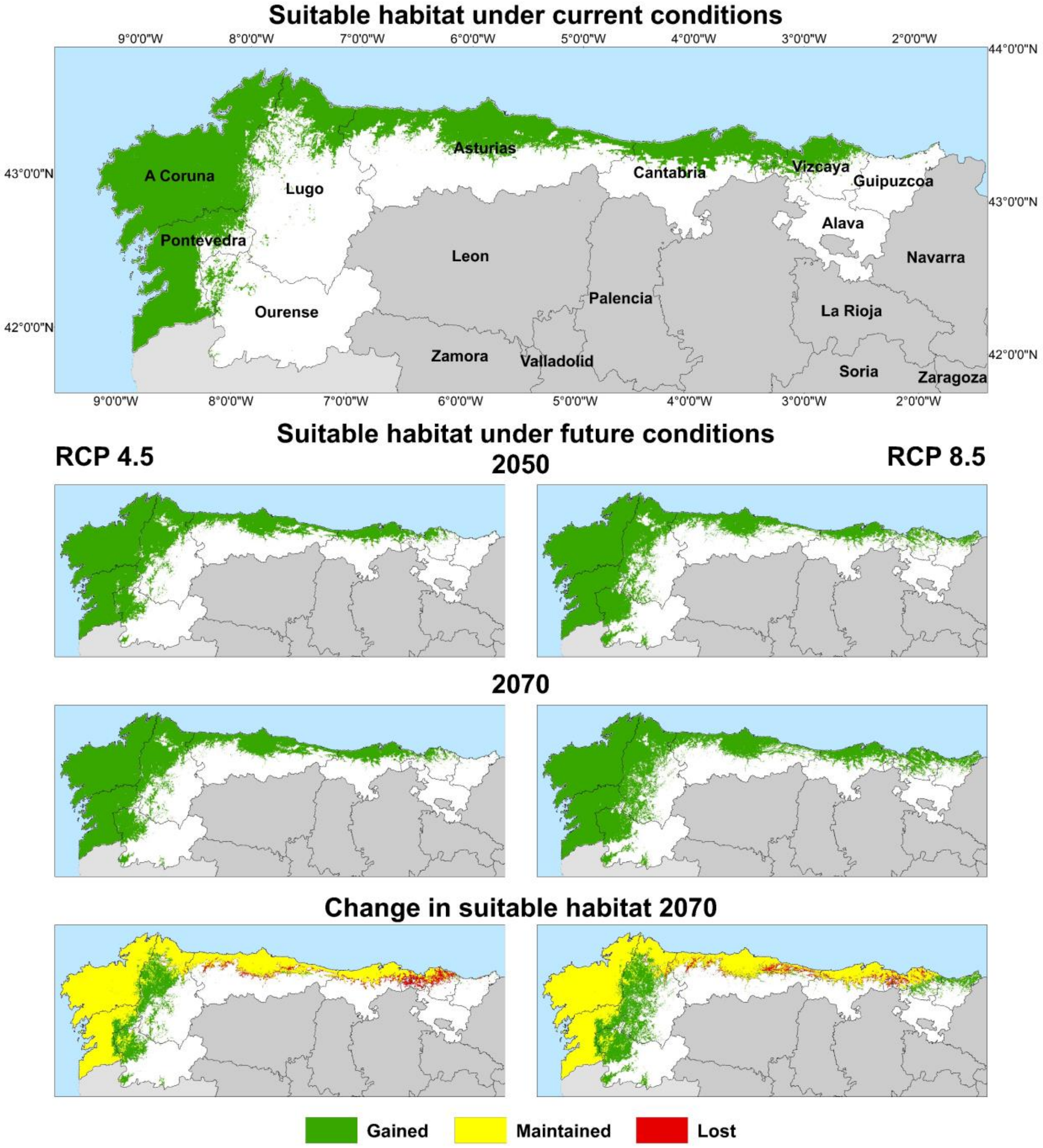
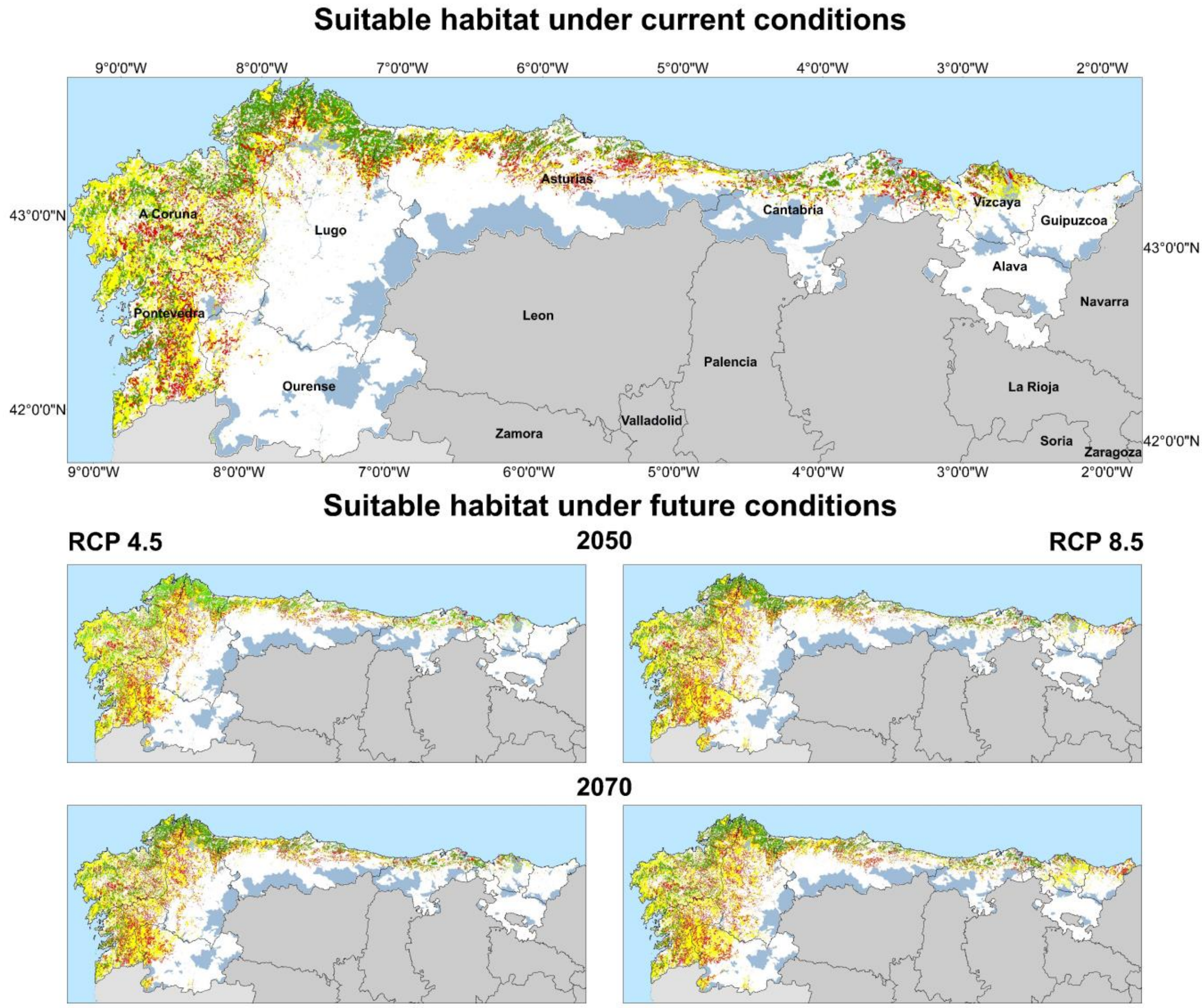
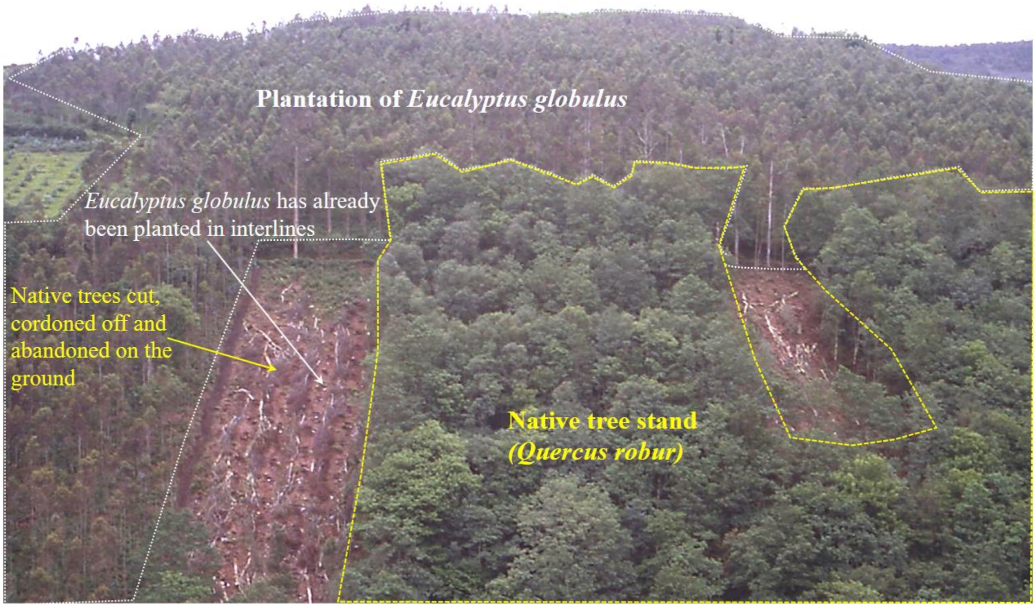

Suitable habitat under current conditions
9°0'0"W
8°0'0"W
7°0'0"W
6°0'0"W
5°0'0"W
4°0'0"W
3°0'0"W
2°0'0"W
44°0'0"N
43°0'0"N
42°0'0"N
A Coruna
Lugo
Asturias
Cantabria
Vizcaya
Guipuzcoa
Alava
Navarra
Pontevedra
Leon
Palencia
La Rioja
Ourense
Zamora
Valladolid
Soria
Zaragoza
Suitable habitat under future conditions
RCP 4.5
2050
RCP 8.5
2070
Change in suitable habitat 2070
🟩 Gained
🟨 Maintained
🟥 Lost

Fig. 4.



<u>Green shading</u>: **EUGL$_{SNFI4.5}$**: current distribution of *E. globulus* according to SNFI4.5. <u>Red shading</u>: **SH$_{NBf}$:** potential expansion area of eucalypts in current native broadleaved forests (CLC2018 code 311 (Broad-leaved forest) minus EU$_{SNFI4.5}$). <u>Yellow shading</u>: **SH$_{FSA}$**: potential area of expansion of *E. globulus* in other natural and semi-natural areas. <u>Blue shading</u>: Natural Protected Areas (NPAs).

Fig 5.


Plantation of Eucalyptus globulus
Eucalyptus globulus has already been planted in interlines
Native trees cut, cordoned off and abandoned on the ground
Native tree stand (Quercus robur)

SUPPLEMENTARY MATERIAL

Supplementary Table S1
Supplementary Figure S1
Supplementary Figure S2

Table S1. Habitat metrics for the current distribution of eucalypts and the five suitable habitats categories.

	Autonomous Community	Galicia				Asturias	Cantabria	Euskadi		
	Province	**Pontevedra**	**A Coruña**	**Lugo**	**Ourense**	**Asturias**	**Cantabria**	**Álava**	**Vizcaya**	**Guipuzcoa**
SH_{GROSS}	**Ele**	293.25	298.87	345.65	420.7	232.05	169.93	189.69	178.6	204.72
	Lat	42.47	43.05	43.44	42.32	43.44	43.34	43.19	43.32	43.32
	Area	359801.43	742312.4	187320.14	28697.108	378800.116	188163.979	609.491	90680.293	1957.271
	MPA	3508.43	117758.1	349.72	128	1796.39	3548.23	29.69	600.08	47.71
	LPI	82.58	97.52	14.98	1.89	36.11	36.5	0.05	38.55	0.43
	AI	97.57	98.79	88.89	72.71	95.27	96.92	52.94	91.77	64.24
SH_{NFL}	**Area**	122493.96	272450.61	51975.59	7221.22	176020.06	104893.94	255.66	38769.44	505.63
	MPA	114.37	105.47	29.63	16.1	110.7	225.92	13.56	94.33	10.74
	LPI	5.3	9.75	1.96	2.8	24.08	41.67	9.94	25.05	4.81
	AI	94.49	94.15	92.97	90.26	95.3	96.81	92.69	95.73	91.49
SH_{NET}	**Area**	237307.47	469861.79	135344.55	21475.89	202780.06	83270.04	353.83	51910.86	1451.64
	MPA	41.55	365.64	92.06	38.83	131.17	196.78	12.05	101.12	25.02
	LPI	297.2	55	55.03	24.33	22.37	8.18	16.21	29.31	23.18
	AI	97.16	96.58	97.02	94.72	95.82	96.01	92.99	96.12	94.67
$EUGL_{SNFI4.5}$	**Area**	48924.67	166240.57	61197.78	178.67	54583.73	33346.71	0.00	8385.58	12.99
	MPA	20.85	23.79	51.54	3.38	19.57	22.5	0	4.65	1.85
	LPI	0.68	4.85	25.92	0.1	0.97	1.03	0	0.92	0.32
	AI	89.77	90.35	93.33	81.89	88.96	91.46	0	83.63	80
SH_{NBF}	**Area**	66033.67	82944.76	28762.99	7678.69	69179.70	27729.85	39.28	13562.98	424.78
	MPA	9.83	5.25	4.52	16.9	5.99	5.51	6.06	14.91	11.78
	LPI	1.17	0.3	1	1.8	0.81	0.5	60.625	1.04	5.89
	AI	89.39	86.85	86.34	90.82	87.46	87.57	85.36	89.58	91.53
SH_{FSA}	**Area**	122349.13	220676.46	45383.78	13618.53	79016.63	22193.47	314.56	29962.30	1013.86
	MPA	32.24	15.09	10.84	20.07	19.66	10.94	10.03	26.47	18.11
	LPI	4.7	2.38	1.13	7.44	2.28	0.51	13.78	10.17	15.74
	AI	94.43	92.67	91.37	92.8	92.94	91.76	91.5	92.73	94.09

SH_{GROSS}: total area of suitable habitat. **SH_{NFL}**: area of suitable habitat in non-forest land. **SH_{NET}**: surface area of CLCf included in suitable habitat (SH_{GROSS} - SH_{NFL}). **$EUGL_{SNFI4.5}$**: current total area occupied by *E. globulus*. **SH_{NBF}**: potential expansion of eucalypt in current native broadleaved forest (CLC2018 code 311 (Broadleaved forest) minus $EUGL_{SNFI4.5}$ and minus surface of *Acacia* sp. formations). **SH_{FSA}**: area of potential expansion in other natural and semi-natural areas (SH_{NET} - SH_{NBF} - $EUGL_{TOTAL}$). **Ele**: elevation (m.a.s.l.). **$EUGL_{SNFI4.5}$**: area currently occupied by eucalyps. **Lat**: latitude (degree), **Area**: total surface area (ha). **MPA**: mean patch area (ha). **LPI**: largest patch index (%). **AI**: aggregation index (%).

11. Supplementary Figure captions

Figure S1. Distribution of the climatic variables included in the model that contributed to explaining the distribution under five scenarios in Asturias, Cantabria and Euskadi: (1) the current reference period; (2) 2050 under the RCP 4.5 emissions scenario; (3) 2050 under the RCP 8.5 emissions scenario; (4) 2070 under the RCP 4.5 emissions scenario; and (5) 2070 under the RCP 8.5 emissions scenario. The variables shown are the five presenting a relative importance higher 50%.

Figure S2. Distribution of the climatic variables included in the model that contributed to explaining the distribution under five scenarios in Galicia: (1) the current reference period; (2) 2050 under the RCP 4.5 emissions scenario; (3) 2050 under the RCP 8.5 emissions scenario; (4) 2070 under the RCP 4.5 emissions scenario; and (5) 2070 under the RCP 8.5 emissions scenario. The variables shown are the five with a relative importance higher 50%.

Figure S1

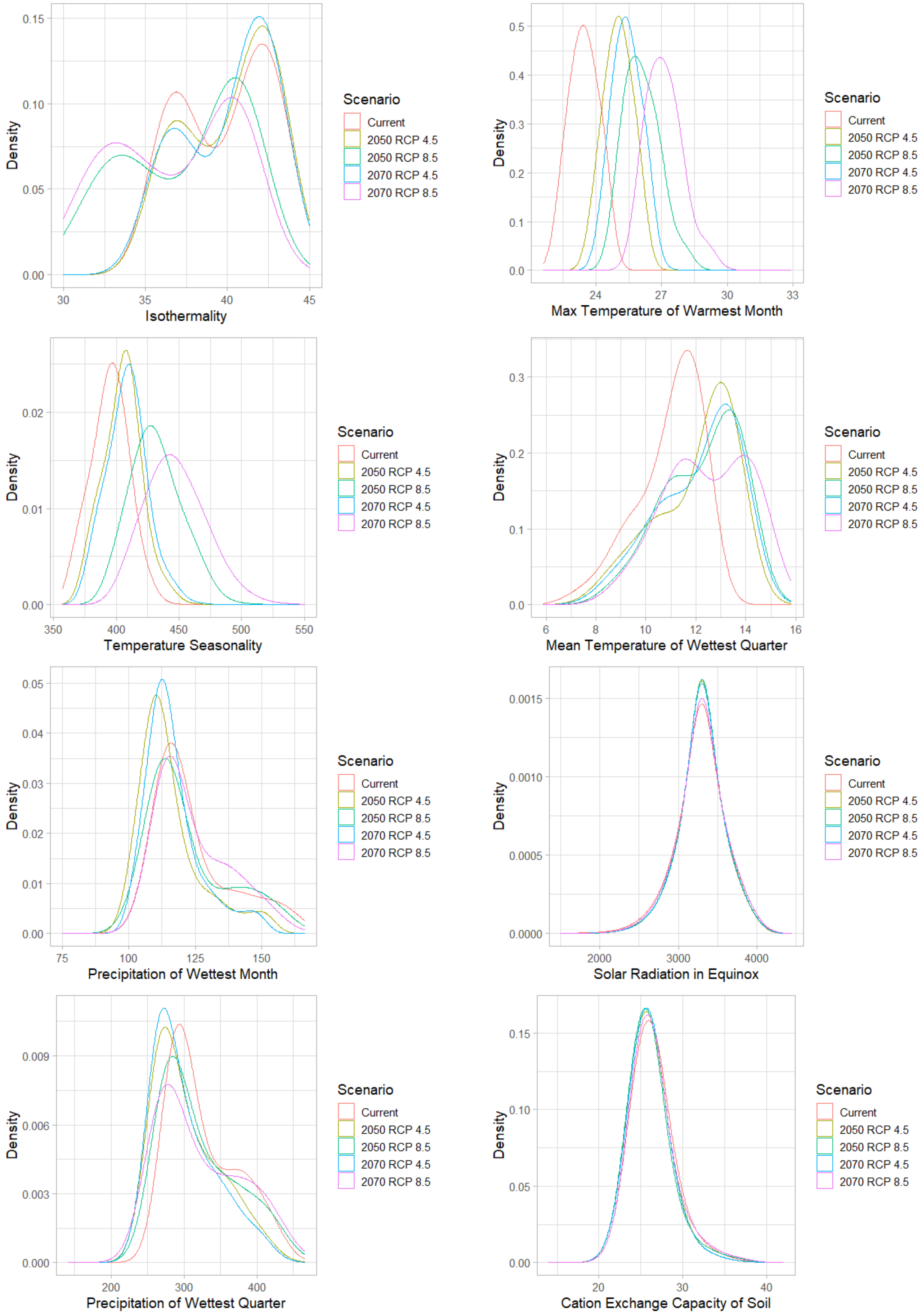
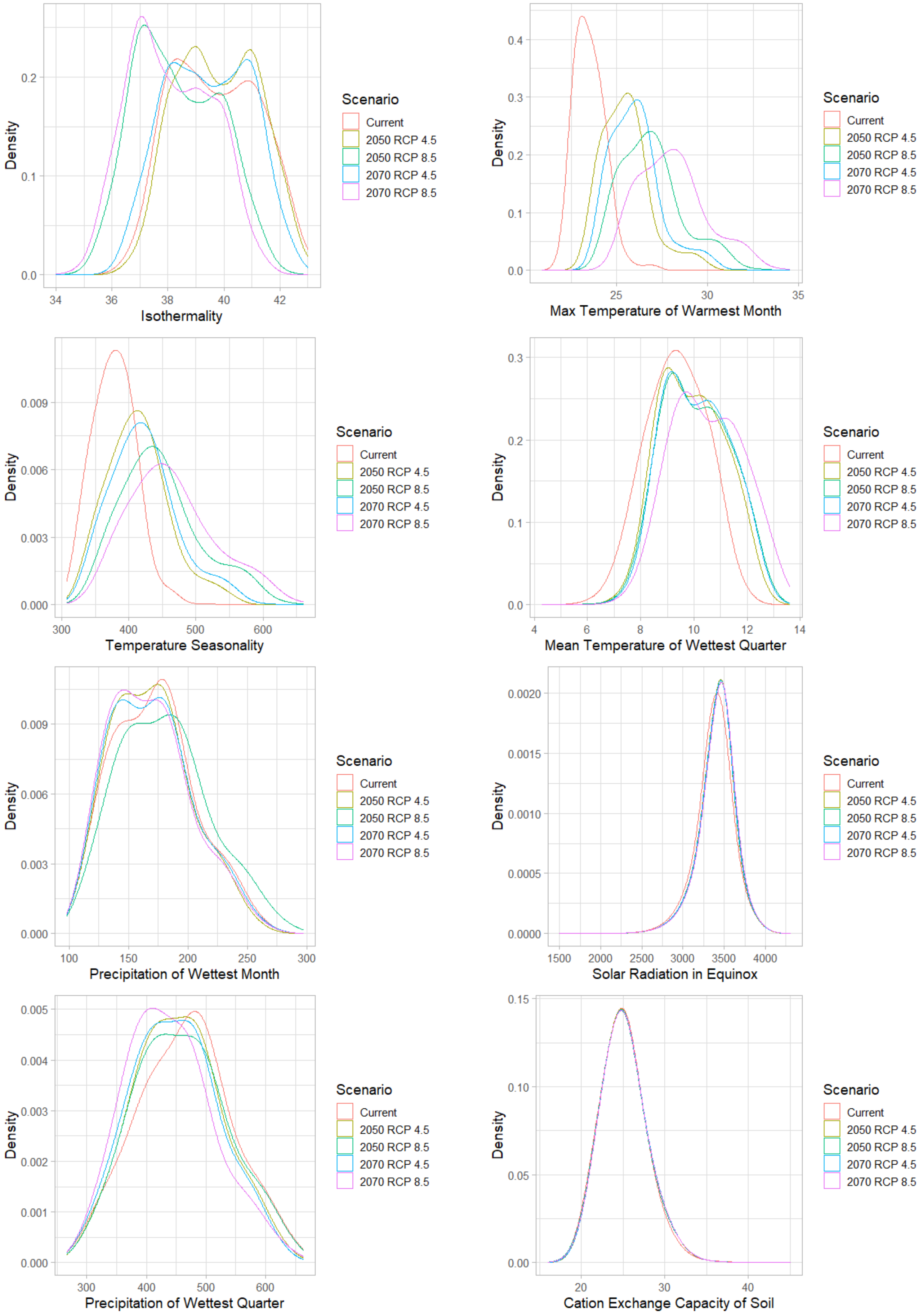

Density
0.15
0.10
0.05
0.00
30
35
40
45
Isothermality
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Density
0.5
0.4
0.3
0.2
0.1
0.0
24
27
30
33
Max Temperature of Warmest Month
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Density
0.02
0.01
0.00
350
400
450
500
550
Temperature Seasonality
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Density
0.3
0.2
0.1
0.0
6
8
10
12
14
16
Mean Temperature of Wettest Quarter
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Density
0.05
0.04
0.03
0.02
0.01
0.00
75
100
125
150
Precipitation of Wettest Month
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Density
0.0015
0.0010
0.0005
0.0000
2000
3000
4000
Solar Radiation in Equinox
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Density
0.009
0.006
0.003
0.000
200
300
400
Precipitation of Wettest Quarter
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Density
0.15
0.10
0.05
0.00
20
30
40
Cation Exchange Capacity of Soil
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5

Figure S2


Density
Isothermality
34
36
38
40
42
0.0
0.1
0.2
Max Temperature of Warmest Month
25
30
35
0.0
0.1
0.2
0.3
0.4
Temperature Seasonality
300
400
500
600
0.000
0.003
0.006
0.009
Mean Temperature of Wettest Quarter
4
6
8
10
12
14
0.0
0.1
0.2
0.3
Precipitation of Wettest Month
100
150
200
250
300
0.000
0.003
0.006
0.009
Solar Radiation in Equinox
1500
2000
2500
3000
3500
4000
0.0000
0.0005
0.0010
0.0015
0.0020
Precipitation of Wettest Quarter
300
400
500
600
0.000
0.001
0.002
0.003
0.004
0.005
Cation Exchange Capacity of Soil
20
30
40
0.00
0.05
0.10
0.15
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5