

# Provisioning forest and conservation science with high-resolution maps of potential distribution of major European tree species under climate change

Debojyoti Chakraborty, Norbert Móricz, Ervin Rasztovits, Laura Dobor, Silvio Schueler

# ▶ To cite this version:

Debojyoti Chakraborty, Norbert Móricz, Ervin Rasztovits, Laura Dobor, Silvio Schueler. Provisioning forest and conservation science with high-resolution maps of potential distribution of major European tree species under climate change. Annals of Forest Science, 2021, 78 (2), pp.26. 10.1007/s13595-021-01029-4. hal-03621137

HAL Id: hal-03621137

 $\rm https://hal.science/hal-03621137$ 

Submitted on 28 Mar 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

#### **DATA PAPER**



# Provisioning forest and conservation science with high-resolution maps of potential distribution of major European tree species under climate change

Debojyoti Chakraborty<sup>1</sup> · Norbert Móricz<sup>2</sup> · Ervin Rasztovits<sup>3</sup> · Laura Dobor<sup>4</sup> · Silvio Schueler<sup>1</sup>

Received: 29 July 2020 / Accepted: 10 January 2021 / Published online: 22 March 2021 © The Author(s) 2021

#### **Abstract**

•Key message We developed a dataset of the potential distribution of seven ecologically and economically important tree species of Europe in terms of their climatic suitability with an ensemble approach while accounting for uncertainty due to model algorithms. The dataset was documented following the ODMAP protocol to ensure reproducibility. Our maps are input data in a decision support tool "SusSelect" which predicts the vulnerability of forest trees in climate change and recommends adapted planting material. Dataset access is at <a href="https://doi.org/10.5281/zenodo.3686918">https://doi.org/10.5281/zenodo.3686918</a>. Associated metadata are available at <a href="https://metadata-afs.nancy.inra.fr/geonetwork/srv/fre/catalog.search#/metadata/fe79a36d-6db8-4a87-8a9f-c72a572b87e8">https://metadata-afs.nancy.inra.fr/geonetwork/srv/fre/catalog.search#/metadata/fe79a36d-6db8-4a87-8a9f-c72a572b87e8</a>.

**Keywords** biomod2 · Ensemble species distribution model · ODMAP

# 1 Background

Climate change is likely to cause widespread shifts in the composition and range of plant communities worldwide (Scheffers et al. 2016). For long-living communities such as forests, such change may lead to a drastic decline in their ability to support multiple ecosystem services (Maroschek et al. 2009; Härtl et al. 2016; Mina et al.

Handling Editor: Marianne Peiffer

Contribution of the co-authors DC: running the data analysis, writing the paper, SS: Research conception, coordination, and supervision writing the paper, NM: Initial model runs, ER: Initial model runs, LD: climate data provision

- Debojyoti Chakraborty debojyoti.chakraborty@bfw.gv.at
- Austrian Research Centre for Forests, Seckendorff-Gudent Weg. 8, 1131 Vienna, Austria
- Department of Ecology and Forest Management, Forest Research Institute, Sárvár, 9600 Sopron, Hungary
- <sup>3</sup> Sopron, Hungary
- Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 21 Prague 6, Czech Republic

2017). In Europe, the effects of climate change on forests may include changes in forest productivity (Reyer et al. 2014), changes in the distribution of tree species (Dyderski et al. 2018; Thurm et al. 2018), the economic value of forests (Hanewinkel et al. 2013), effects of intensifying disturbance regimes (Seidl et al. 2011, 2014), and droughts (Allen et al. 2010).

As such, there has been considerable interest in estimating the potential distribution of tree species under scenarios of climate change. Species distribution models (SDMs), often referred to as ecological niche models (ENMs), are the most widely used tools for this purpose (Sykes et al. 1996; Zimmermann et al. 2010; Guisan et al. 2013; Dyderski et al. 2018), because they predict the potential distribution of species by exploiting the correlation between the known occurrence of a species and corresponding environmental conditions.

In the recent decades, SDMs have evolved and were applied for a wide range of questions such as to predict species range in the future (Sykes et al. 1996; Thuiller et al. 2008; Dyderski et al. 2018), to test hypotheses about species distribution limits (Kreyling et al. 2015), to develop conservation and management strategies in climate change (Guisan et al. 2013; Hamann and Aitken 2013; Mcshea 2014; Schueler et al. 2014), and understand the role of genetic variation in tree species distributions (O'Neill et al.



2008; Benito Garzón et al. 2011; Valladares et al. 2014; Chakraborty et al. 2019; Garate-Escamilla et al. 2019).

Despite the recent improvements and widespread use, the free and unrestricted utilization of SDMs in the applied forest and conservation science is often limited due to inadequate documentation and reporting of the predictions and uncertainties. Therefore, Zurell et al. (2020) proposed a reporting protocol known as ODMAP (Overview, Data, Model, Assessment, and Prediction), which offers a standardized way of communicating the results/outputs from SDMs by describing the objectives, model assumptions, scaling issues, data sources, model workflow, model predictions, and uncertainty.

Here we present a dataset on the potential distribution of seven widely occurring tree species of Europe for current and projected future climate scenarios. To ensure transparent reporting and reproducibility, we described the dataset according to the ODMAP protocol suggested by Zurell et al. (2020). The following sections describe the basic elements of the dataset, while the detailed metadata according to ODMAP (Zurell et al. 2020) is presented in Table 2 in Appendix.

#### 2 Methods

#### 2.1 Species occurrence data

Current occurrence (presence and absence) of seven major stand forming tree species in Europe (Table 1) was obtained from the EU-Forest dataset (Mauri et al. 2017). These species are known to form stands in a wide range

of forest types across Europe (European Environmental Agency 2006) and are also economically important (Hanewinkel et al. 2013). The Mauri et al. (2017) dataset is one of the most exhaustive, harmonized European tree species occurrence (presence) data available till date, which combines three existing datasets: the Forest Focus (Hiederer et al. 2011), Biosoil (Houston Durrant et al. 2011), and national forest inventories. In our case, the geographic locations of the target species in the EU-Forest dataset were assumed to be true presences, while the presence locations of other target species were assumed to be the absence locations. To ensure that the absence locations are not only climatically dissimilar but also geographically distant from the observed presence locations, we developed the so-called pseudoabsences according to Senay et al. (2013). This is a three-step approach: (i) specifying a geographical extent outside the observed presences, (ii) environmental profiling of the absences outside this geographic extent, and (iii) k-means clustering of the environmental profiles and selecting random samples within each cluster. In our case, a 2-degree buffer was found to be optimum following Senay et al. (2013). The absence locations outside this geographic extent were classified into 10-15 environmentally dissimilar clusters according to the k-means clustering algorithm. The numbers of absence clusters for each species were determined from the elbow of the plot of total within-cluster sum of square (WSS) and number of clusters. The number of pseudoabsence locations was further reduced by randomly selecting a sample of locations defined by the 95% confidence interval from each of the absence clusters. This approach was used

Table 1 Occurrence (presence and absence points) for the seven tree species obtained from Mauri et al. (2017) and model evaluation statistics. The model evaluation based on mean ROC, TSS, sensitivity, and specificity of the models used to develop the ensemble predictions. For detailed model evaluation see Table 5 for the seven tree species

	Occurrenc	Occurrence data Model evaluation					
Species	Presence	Absence	Criteria	Testing data	Evaluating data	Sensitivity	Specificity
A alba	9895	579,088	ROC	0.98	0.98	94.74	96.67
F sylvatica	38,693	550,290	ROC	0.95	0.95	92.09	88.19
L decidua	14,747	574,236	ROC	0.96	0.96	94.06	92.28
P abies	61,210	527,773	ROC	0.95	0.95	93.47	90.08
P sylvestris	70,852	518,131	ROC	0.94	0.94	93.03	87.01
Q petraea	20,929	568,054	ROC	0.94	0.94	91.74	86.45
Q robur	24,809	564,174	ROC	0.97	0.97	92.96	93.36
A alba	9895	579,088	TSS	0.92	0.91	94.78	96.44
F sylvatica	38,693	550,290	TSS	0.81	0.80	91.79	88.40
L decidua	14,747	574,236	TSS	0.86	0.86	94.19	92.02
P abies	61,210	527,773	TSS	0.84	0.83	93.16	90.32
P sylvestris	70,852	518,131	TSS	0.80	0.80	93.18	86.72
Q petraea	20,929	568,054	TSS	0.79	0.78	91.83	86.19
Q robur	24,809	564,174	TSS	0.86	0.86	93.21	93.04



to generate pseudo-absence for all seven species. The resultant dataset was used to calibrate the SDMs with the biomod2 platform (Thuiller et al. 2016).

#### 2.2 Climate data

Biologically relevant climate variables were obtained from the ECLIPS 2.0 dataset (Chakraborty et al. 2020a, b). This dataset was developed from dynamically downscaled, and bias-corrected regional climate model results from the EURO-CORDEX with a resolution of 30 arcsec. The EURO-CORDEX (www.eurocordex.net) is an initiative of the World Climate Research Program (Giorgi et al. 2009) for coordinating dynamic regional downscaling of the global climate projections from the CMIP5 (Coupled Model Intercomparison Project Phase 5) (Jacob et al. 2014). All projections were corrected for bias using a distribution scaling method (Yang et al. 2010) to produce 0.11 × 0.11° resolution gridded data for daily mean, minimum, and maximum nearsurface air temperature and precipitation. We further refined this  $0.11 \times 0.11^{\circ}$  resolution bias-corrected data to 30 arcsec using the delta algorithm for spatial downscaling (Ramirez-Villegas and Jarvis 2010; Moreno and Hasenauer 2016). With this approach, we developed a gridded dataset for 80 climate variables (Table 3 in Appendix) for historic climate (1961–1990) and three future time frames which include averages of (2041–2060, 2061–2080, and 2081–2100) for two Representative Concentration Pathway (van Vuuren et al. 2011), RCP 4.5 and RCP 8.5. The RCP 4.5 or the moderate scenario assumes a 650-ppm atmospheric CO<sub>2</sub> concentration and a 1.0–2.6-°C increase in annual temperature by 2100, whereas in RCP 8.5, a pessimistic scenario assumes a 1350-ppm CO<sub>2</sub> and 2.6-4.8-°C increase in annual temperature by 2100 (van Vuuren et al. 2011). The ECLIPS 2.0 dataset is available at https://doi. org/10.5281/zenodo.3952159.

#### 2.3 Variable selection

From the list of potential predictor variables (Table 3 in Appendix), the ones which explain most of the variation in the observed presence and absences of each species were selected with a recursive feature elimination approach (RFE) implemented within the Random forest algorithm (Breiman 2001). Within the RFE approach,

the variables were eliminated iteratively, starting from the full set of potential predictors and retaining only those variables that reduce the mean square error over random permutations of the same variable. The variables which were linearly correlated with other variables and had a variance inflation factors VIF > 5, a commonly used threshold in detecting mulicollinearity (Craney and Surles 2002; Thompson et al. 2017), were identified. The identified collinear variables with the lower value according to the Akaike Information Criteria (AIC) (Akaike 1974) were retained for further model development. This subset of uncorrelated climate variables (Table 4 in Appendix) was used as predictor variables for developing the ensemble species distribution models.

#### 2.4 Ensemble species distribution models

To model the potential distribution of the seven European tree species, an ensemble distribution modeling approach, implemented through the R package, biomod2 (Thuiller et al. 2016), was used. biomod2 offers a computational platform for multi-method modeling that generates models of species' potential distribution for each species. The model algorithms include GLM (Generalized Linear Models), GAM (Generalized Additive Models), GBM (Generalized Boosted regression Models), CTA (Classification Tree Analysis), ANN (Artificial Neural Networks), SRE (Surface Range Envelop or BIOCLIM), FDA (Flexible Discriminant Analysis), MARS (Multivariate Adaptive Regression Spline), RF (Random Forest for classification and regression), and MAXENT. Tsuruoka. Hence, biomod2 combines the strengths of multiple modeling algorithms while accounting for their uncertainties. We used biomod2 default settings for all the modeling algorithms (Thuiller et al. 2016). Each model algorithm predicted the probability of the potential distribution for each species. Such probabilities predicted from the individual models were ensembled into a consensus model by combining the median probability over the selected models with true skill statistics threshold (TSS > 0.7) (Allouche et al. 2006; Coetzee et al. 2009). The median was chosen because it is known to be less sensitive to outliers than the mean. The estimated ensemble model predictions were presented as GeoTIFF rasters. These raster files are available at https://doi. org/10.5281/zenodo.3686918.



#### 2.5 Model evaluation and uncertainty analysis

Model evaluation was carried by splitting the occurrence dataset into 75% for model training and 25% for model testing. Besides, biomod2 allows specifying the number of runs for each combination of training and testing data. Therefore, 10 independent runs, each with a randomly selected set of training and test data, were implemented.

For each such model run as well as the final ensemble models, the model evaluation statistics were recorded. These statistics were true skill statistics (TSS) and area under the relative operating characteristic (ROC), model sensitivity (the ability of the model to predict true presences), and model specificity (the ability of the model to predict the true absences). TSS takes into account both omission and commission errors and ranges also from -1 to +1, not being affected by prevalence as KAPPA (Allouche et al. 2006). TSS values ranging from 0.2 to 0.5 were considered poor, from 0.6 to 0.8 useful, and values larger than 0.8 were good to excellent (e.g., Coetzee et al. 2009). Prediction accuracy is considered to be similar to random for ROC values lower than 0.5; poor, for values in the range 0.5–0.7; fair in the range 0.7-0.9; and excellent for values greater than 0.9 (Pontius and Parmentier 2014).

Model uncertainty was also estimated in terms of coefficient of variation (CV) among the predictions of the individual models. The estimated CVs are also presented as GeoTIFF rasters where each cell corresponds to a CV value, whereby higher and lower CV values indicate higher and lower uncertainties, respectively, in the ensemble model. These raster files are available at https://doi.org/10.5281/zenodo.3686918.

In addition to internal evaluation, the model predictions were also tested against independent data on European Forest Genetic Conservation Units (GCU) (Lefèvre et al. 2013). The geographic locations of the 3354 genetic conservation units (Fig. 3 in Appendix) were used to extract the predicted probability of occurrence from the models for the seven target species for the period 1961–1990. The ensemble models were used to predict the distribution of the seven target species at each GCU location. Predicted probability < 60 were assumed to be, "incorrectly predicted," whereas those > 60% were treated as "correctly predicted" following Dyderski et al. (2018). For most species, the incorrectly classified GCUs are those located in the southeastern part of their potential distribution (Fig. 3 in Appendix).

# 3 Access to the data and metadata description

The dataset is accessible through https://doi.org/10.5281/zenodo.3686918. Associated metadata are available at https://metadata-afs.nancy.inra.fr/geonetwork/srv/fre/catalog.search#/metadata/fe79a36d-6db8-4a87-8a9f-c72a572b87e8

#### 4 Technical validation

In general, for all species, a high correlation was observed between the predictive performance of the models calibrated with both training and evaluation data with mean TSS ranging from 0.79 to 0.92 and mean ROC ranging from 0.92 to 0.98 (Table 1). Average sensitivity or the ability of the models to predict true presences across all species and models range from 95 to 98% and average specificity or the ability of the models to predict true absences range 86–96% (Table 1). Detailed performance of individual models can be found in Table 5 in Appendix.

Model evaluation against independent data reveals that out of the total 3354, 80–96% of the species occurrence in the European genetic conservation unit (GCU) dataset was correctly predicted by our ensemble SDMs (Table 6 in Appendix).

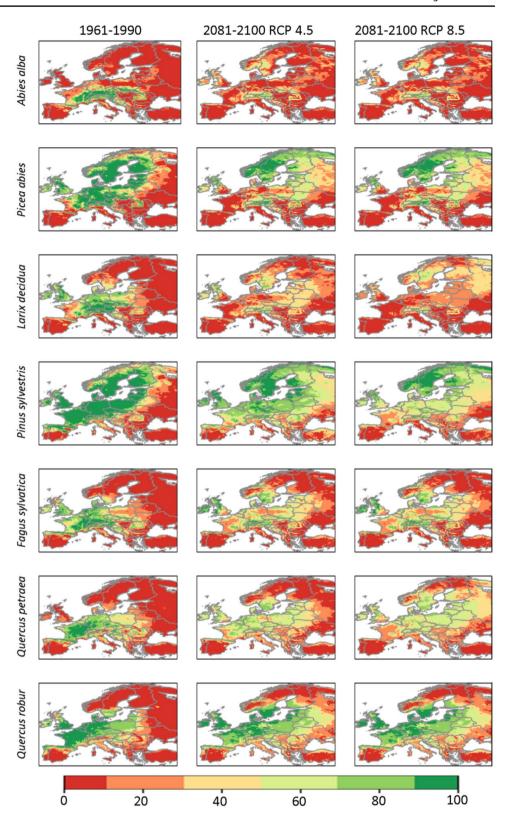
The ensemble SDMs predicts a substantial change in the potential distribution of the seven target species (Fig. 1). A general trend of a northward shift in potential climate suitability (probability > 60%) was predicted, as also observed by recent studies such as Dyderski et al. (2018). Median uncertainty represented by the coefficient of variation between individual models varies between 6 and 15% and with *Larix decidua* and *Abies alba* having higher prediction uncertainty compared to other species (Fig. 2).

## 5 Reuse potential and limits

The dataset is currently being used to develop a decision support tool, SusSelect Smartphone app https://play.google.com/store/apps/details?id=com.topolynx.susselect&hl=en, which calculates the vulnerability of tree species under climate change. The dataset is also being used to develop an Integrated Toolbox that combines tools from Interreg CE, Horizon 2020, and EU Life projects. This integrated toolbox (TEACHER-CE) is under development and focuses on climate-proof management of water-related issues such as floods, heavy rain, and drought risk prevention, small water retention measures, and protection of water resources through sustainable land-use management. For details see: https://www.interreg-central.eu/Content.Node/TEACHER-CE.html.



Fig. 1 Potential distribution of seven European tree species under the historical period (1961–1990) and predicted future scenario of 2080–2100 under RCP 4.5 and RCP 8.5





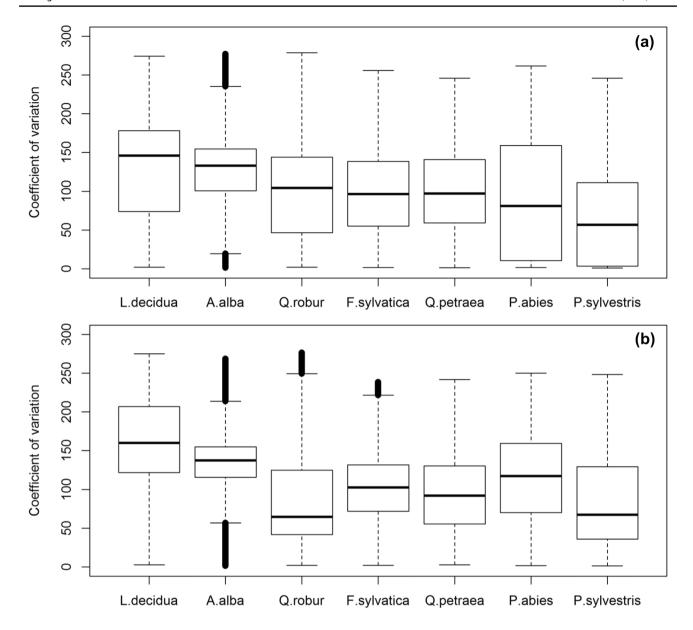


Fig. 2 Uncertainly of predictions for the seven target tree species under a current climate (1961–90) and b RCP 8.5 (1981–2100) expressed as the coefficient of variation

Ecological niche models or SDMs assume that the relation between climatic drivers and the species distribution remains constant also in climate change. This assumption needs to be taken into account while interpreting the results of the paper. change (Version v1) [data set]. Zenodo. http://doi.org/10. 5281/zenodo.3686918

#### 6 Dataset citation

Chakraborty D, Móricz N, Rasztovits E, Dobor L, Schueler S (2020). Provisioning forest and conservation science with European tree species distribution models under climate

# **Appendix**

Provisioning forest and conservation science with highresolution maps of potential distribution of major European tree species under climate change.



ODMAP elements	Contents
Overview	
Authorship	Authors: Debojyoti Chakraborty, Norbert Móricz, Ervin Rasztovits, Laura Dobor, Silvio Schueler Contact email: debojyoti.chakraborty@bfw.gv.at Title:  DOI:
Model objective	SDM Objective: forecast/transfer Target output: probability of occurrence of target tree species
Taxon	Seven tree species of Europe: Abies alba, Fagus sylvatica, Larix decidua, Picea abies, Pinus sylvestris, Quercus petraea, Quercus robur
Location	Europe
Scale of analysis	Spatial extent (Lon/ Lat): Longitude: - 32.65000°E, -69.44167°E Latitude: 30.877982°N, -71.57893°N Spatial resolution: 30 arcsec Temporal resolution: We modeled for historic climate (1961–1990) and three future time frames which include averages of (2041–2060, 2061–2080, and 2081–2100). The predictions were done for two Representative Concentrations RCP 4.5 and RCP 8.5
Biodiversity data overview	Observation type: standardized monitoring Response data type: presence/absence data
Type of predictors	Climatic
Conceptual model/hypotheses	A large body of scientific studies indicate that climate is one of the major drivers of the distribution of tree species at the continental scale. We exploited this correlation between species' current occurrence and climate to develop SDMs that predict the potential distribution of the target tree species
Assumptions	We assumed that species are at pseudo-equilibrium with the environment. The source of the presence/absence data (Mauri et al. 2017) used in this study is largely from national forest inventories where tree individuals below a certain diameter at breast height are not recorded. We assume that this data collection procedure did not bias our occurrence data  Since our occurrence dataset covers the whole current distribution of the target species, which represents both current and likely future climate of Europe, we safely assumed that the species retain their niches across space and
	time and the current occurrence~climate correlation remains stable when predicting the models for future climate
SDM algorithms	Algorithms: We selected 10 modeling algorithms: GLM (Generalized Linear Models), GAM (Generalized Additive Models), GBM (Generalized Boosted regression Models), CTA (Classification Tree Analysis), ANN (Artificial Neural Networks), SRE (Surface Range Envelop or BIOCLIM), FDA (Flexible Discriminant Analysis), MARS (Multivariate Adaptive Regression Spline), RF (Random Forest for classification and regression), and MAXENT. Tsuruoka. These model algorithms were implemented through an ensemble model platform biomod2 (Thuiller et al. 2016)  Model complexity: The individual models were run using the standard default settings of biomod2 that are designed to balance model complexity and overfitting
	Ensembles: The prediction of individual model algorithms were ensembled through biomod2 (Thuiller et al. 2016)



#### Table 2 (continued) ODMAP elements Contents Model workflow The model workflow includes the following: 1. Data cleaning and generation of pseudo absences 2. Finding the best climate variables to fit the models 2. Model running through biomod2 platform 3. Ensemble prediction 4. Generation of the maps as gridded 30 arcsec rasters Software Software: All analyses were conducted using R version 3.3.2 (R Core Team 2016). Packages used: biomod2 (Thuiller et al. 2016), Random Forest (Breiman 2001),

Data availability:

Presence absence data are available from Mauri et al. (2017)

Climate data is available from

Chakraborty D, Dobor L, A, Hlásny T, Schueler S (2020)

High-resolution gridded climate data for Europe based on bias-corrected EURO-CORDEX: the ECLIPS-2.0 dataset [Zenodo: https://doi.org/10.5281/zenodo.3952159.]

Data

Biodiversity data

Taxon names: Abies alba, Fagus sylvatica, Larix decidua, Picea abies, Pinus sylvestris, Quercus petraea, Quercus

Ecological level: Species-level

Data source:

Species presence-absence data was obtained from the EU-Forest dataset (Mauri et al. 2017). The dataset harmonizes European tree occurrence from National Forest inventories (NFI), Forest Focus (Hiederer et al. 2011), and Biosoil datasets (Houston Durrant et al. 2011). A major part of the data arises from the NFI data (96%) while 4% contributed by Forest Focus (Hiederer et al. 2011), Biosoil datasets (Houston Durrant et al. 2011)

Sampling design: The background data included in the EU-Forest (Mauri et al. 2017) varied in their sampling intensity and design. This data was harmonized and aggregated to a spatial resolution of 1 square kilometer, in line with an INSPIREcompliant 1-km × 1-km grid

Sample size

The dataset includes a total of 1,000,525 occurrence records at a spatial resolution of 1×1 km (Mauri et al. 2017)

Data filtering: Form the EU-Forest dataset we obtained

412,2881 occurrence records about the seven target species

Presence-absence data:

In our case the geographic locations of the target species in the EU-Forest dataset was assumed to be true presences, while the remaining locations of occurrence of other species were assumed to be the absence locations

To ensure that the absence locations are not only climatically dissimilar but also geographically distant from the observed presence locations, we developed the so-called pseudo absences according to Senay et al. (2013). This is a three-step approach: (i) specifying a geographical extent outside the observed presences, (ii) environmental profiling of the absences outside this geographic extent, and (iii) k-means clustering of the environmental profiles and selecting random samples within each cluster. In our case, a 2-degree buffer was found to be optimum following Senay et al. (2013). The absence locations outside this geographic extent were classified into 10-15 (depending on species) environmentally dissimilar clusters according to the k-means clustering algorithm. The number of clusters for each species were determined with a plot of total within-cluster sum of square (WSS) and number of clusters

The number of pseudoabsence locations was further reduced by randomly selecting a sample of locations defined by the 95% confidence interval from each of the clusters. This approach was used to generate pseudoabsence for all the seven species

Data partitioning

The occurrence dataset for each target species was partitioned by splitting into 75% for model training and 25% for model evaluation

Environmental predictors

Predictor variables

Environmental predictors were 80 biologically relevant climate variables comprising of annual, seasonal, and monthly variables

From this list of 80 variables, a small subset of potential predictor variables was selected for each target species during the variable selection process

Data sources:

The spatial resolution of predictor data: 30 arcsec which is roughly equivalent to 1×1 km or lower depending on latitude

The temporal resolution of predictor variable: Historic climate (1961–1990) and three future time frames which include averages of (2041-2060, 2061-2080, and 2081-2100) for two Representative Concentration RCP 4.5 and RCP 8.5 were used for the SDM predictions

Geographic projection: WGS 84 (EPSG: 4326)

Model



# Table 2 (continued)

ODMAP elements	Contents
Variable selection and multi- collinearity	From the list of potential predictor variables (Table 2 in Appendix), the ones which explain most of the variation in the observed presence and absences of each species were selected with a recursive feature elimination approach (RFE) implemented within the Random forest algorithm (Breiman 2001). Within the RFE approach, the variables were eliminated iteratively, starting from the full set of potential predictors (Table 2 in Appendix), and retaining only those variables that reduce the mean square error over random permutations of the same variable. The variables which were linearly correlated with other variables and had a variance inflation factors VIF > 5 as suggested by Booth et al. (1994) were identified, and the ones with the lower value according to the Akaike Information Criteria (AIC) (Akaike 1974) were retained for further model development. This subset of uncorrelated climate variables (Table 3 in Appendix) was used as predictor variables for developing the ensemble species distribution models
Model settings	The models were run with the default settings of biomod2 (Thuiller et al. 2016)
Model estimates	The models estimated median ensemble probability of species occurrence and associated model uncertainty represented by the coefficient of variation
Model ensemble	Predicted probabilities from the individual models for each target species were ensembled as a consensus model which combined the median probability over the selected models with true skill statistics threshold (TSS > 0.7) (Allouche et al. 2006; Coetzee et al. 2009)
Threshold selection	True skill statistics threshold (TSS > 0.7), a commonly used threshold for SDMS (Allouche et al. 2006; Coetzee et al. 2009), was used
Assessment	
Model performance statistics	For each such model run as well as the final ensemble models for each target species, the model evaluation statistics were recorded. These statistics were true skill statistics (TSS) and area under the relative operating characteristic (ROC), model sensitivity (the ability of the model to predict true presences), and model specificity (the ability of the model to predict the true absences). TSS takes into account both omission and commission errors and ranges also from – 1 to + 1, not being affected by prevalence as KAPPA (Allouche et al. 2006). TSS values ranging from 0.2 to 0.5 were considered poor, from 0.6 to 0.8 useful, and values larger than 0.8 were good to excellent (e.g. Coetzee et al. 2009). Prediction accuracy is considered to be similar to random for ROC values lower than 0.5; poor, for values in the range 0.5–0.7; fair in the range 0.7–0.9; and excellent for values greater than 0.9 (Pontius and Parmentier 2014)
Prediction	
Prediction output	Predicted probabilities from the individual models and target species were ensembled as a consensus model which combined the median probability over the selected models with true skill statistics threshold (TSS $> 0.7$ ) (Allouche et al. 2006; Coetzee et al. 2009). The median was chosen because it is known to be less sensitive to outliers than the mean. The estimated ensemble model predictions were presented as GeoTIFF rasters
Uncertainty quantification	Model uncertainty was estimated in terms of coefficient of variation (CV) among the predictions of the individual models. The estimated CVs are also presented as GeoTIFF rasters where each cell corresponds to a CV value whereby higher and lower CV values indicate higher and lower uncertainty respectively in the ensemble model



Table 3 Potential climate variables from the ECLIPS 2.0 dataset (Chakraborty et al. 2020a, b) used to calibrate the ensemble SDMs

Climate variable	Variables	Unit
AHM	Annual heat: moisture index (MAT+10)/(MAP/1000))	
bFFP	The Julian date on which FFP begins	
DDabove18	Degree-days below 18 °C, heating degree-days	
DDabove5	Degree-days above 5 °C, growing degree-days	
DDbelow0	Degree-days below 0 °C, chilling degree-days	
DDbelow18	Degree-days below 18 °C, heating degree-days	
eFFP	The Julian date on which FFP ends	
EMT	Extreme minimum temperature over 30 years	°C
FFP	Frost-free period	Days
MAP	Mean annual precipitation (mm)	°C
MAT	Mean annual temperature (°C)	°C
MCMT	Mean coldest month temperature (°C)	°C
MSP	Mean summer (May to Sept.) precipitation (mm)	°C
MWMT	Mean warmest month temperature (°C)	°C
NFFD	The number of frost-free days	days
PPT_at	Autumn precipitation (mm)	mm
PPT_sm	Summer precipitation (mm)	mm
PPT_sp	Spring precipitation (mm)	mm
PPT_wt	Winter precipitation (mm)	mm
PPT01	Precipitation month 01	mm
PPT02	Precipitation month 02	mm
PPT03	Precipitation month 03	mm
PPT04	Precipitation month 04	mm
PPT05	Precipitation month 05	mm
PPT06	Precipitation month 06	mm
PPT07	Precipitation month 07	mm
PPT08	Precipitation month 08	mm
PPT09	Precipitation month 09	mm
PPT10	Precipitation month 10	mm
PPT11	Precipitation month 11	mm
PPT12	Precipitation month 12	mm
SHM	Summer heat: moisture index ((MWMT)/(MSP/1000))	
Tave_at	Autumn (Sep.–Nov.) mean temperature (°C)	°C
Tave_sm	Summer (Jun.–Aug.) mean temperature (°C)	°C
Tave_sp	Spring (Mar.–May) mean temperature (°C)	°C
Tave_wt	Winter (Dec. (prev. yr)–Feb.) mean temperature (°C)	°C
Tave01	Average temperature month 01	°C
Tave02	Average temperature month 02	°C
Tave03	Average temperature month 03	°C
Tave04	Average temperature month 04	°C
Tave05	Average temperature month 05	°C
Tave06	Average temperature month 06	°C
Tave07	Average temperature month 07	°C
Tave08	Average temperature month 08	°C
Tave09	Average temperature month 09	°C
Tave10	Average temperature month 10	°C
Tave10	Average temperature month 11	°C
Tave12	Average temperature month 12	°C
TD	Temperature difference between MWMT and MCMT(°C)	°C
Tmax_an	Maximum yearly temperature	°C
Tmax_an Tmax_at	Maximum autumn temperature	°C
- mun_ut	maximum addini competature	



# Table 3 (continued)

Climate variable	Variables	Unit
Tmax_sm	Maximum summer temperature	°C
Tmax_sp	Maximum spring temperature	$^{\circ}\mathrm{C}$
Tmax_wt	Maximum winter temperature	$^{\circ}\mathrm{C}$
Tmax01	Maximum temperature 01	$^{\circ}\mathrm{C}$
Tmax02	Maximum temperature 02	$^{\circ}\mathrm{C}$
Tmax03	Maximum temperature 03	$^{\circ}\mathrm{C}$
Tmax04	Maximum temperature 04	$^{\circ}\mathrm{C}$
Tmax05	Maximum temperature 05	$^{\circ}\mathrm{C}$
Tmax06	Maximum temperature 06	$^{\circ}\mathrm{C}$
Tmax07	Maximum temperature 07	°C
Tmax08	Maximum temperature 08	°C
Tmax09	Maximum temperature 09	°C
Tmax10	Maximum temperature 10	$^{\circ}\mathrm{C}$
Tmax11	Maximum temperature 11	$^{\circ}\mathrm{C}$
Tmax12	Maximum temperature 12	$^{\circ}\mathrm{C}$
Tmin_an	Minimum annual temperature	$^{\circ}\mathrm{C}$
Tmin_at	Minimum autumn temperature	$^{\circ}\mathrm{C}$
Tmin_sm	Minimum summer temperature	$^{\circ}\mathrm{C}$
Tmin_sp	Minimum spring temperature	$^{\circ}\mathrm{C}$
Tmin_wt	Minimum winter temperature	$^{\circ}\mathrm{C}$
Tmin01	Minimum temperature 01	$^{\circ}\mathrm{C}$
Tmin02	Minimum temperature 02	$^{\circ}\mathrm{C}$
Tmin03	Minimum temperature 03	$^{\circ}\mathrm{C}$
Tmin04	Minimum temperature 04	$^{\circ}\mathrm{C}$
Tmin05	Minimum temperature 05	$^{\circ}\mathrm{C}$
Tmin06	Minimum temperature 06	$^{\circ}\mathrm{C}$
Tmin07	Minimum temperature 07	$^{\circ}\mathrm{C}$
Tmin08	Minimum temperature 08	$^{\circ}\mathrm{C}$
Tmin09	Minimum temperature 09	$^{\circ}\mathrm{C}$
Tmin10	Minimum temperature 10	$^{\circ}\mathrm{C}$
Tmin11	Minimum temperature 11	$^{\circ}\mathrm{C}$
Tmin12	Minimum temperature 12	$^{\circ}\mathrm{C}$



**Table 4** Climate variables used to calibrate the ensemble SDMs

Acronym	Climate variable	Species
SHM	Summer heat-moisture index	Picea abies
PPT_at	Mean autumn precipitation	Picea abies
FFP	Longest frost-free period	Picea abies
TD	Continentality	Picea abies
MCMT	Mean coldest month temperature	Picea abies
SHM	Summer heat-moisture index	Abies alba
EMT	Extreme minimum temperature	Abies alba
TD	Continentality	Abies alba
SHM	Summer heat-moisture index	Larix decidua
Tave_sm	Average summer temperature	Larix decidua
MWMT	Mean warmest month temperature	Larix decidua
SHM	Summer heat-moisture index	Pinus sylvestris
DDabove18	Days with mean temperature above 18 °C	Pinus sylvestris
Tmax_sp	Maximum spring temperature	Pinus sylvestris
Tave_wt	Average winter temperature	Pinus sylvestris
SHM	Summer heat-moisture index	Fagus sylvatica
DDabove5	Days with mean temperature above 5 °C	Fagus sylvatica
PPT_sp	Mean spring precipitation	Fagus sylvatica
EMT	Extreme minimum temperature	Fagus sylvatica
Tave_sp	Average spring temperature	Fagus sylvatica
DDbelow18	Days with mean temperature below 18 °C	Quercus petraea
PPT_sm	Mean summer temperature	Quercus petraea
MAT	Mean annual temperature	Quercus petraea
DDabove5	Days with mean temperature above 5 °C	Quercus robur
PPT_sm	Mean summer temperature	Quercus robur
FFP	Longest frost-free period	Quercus robur
Tmin_sp	Minimum spring temperature	Quercus robur
MCMT	Mean coldest month temperature	Quercus robur



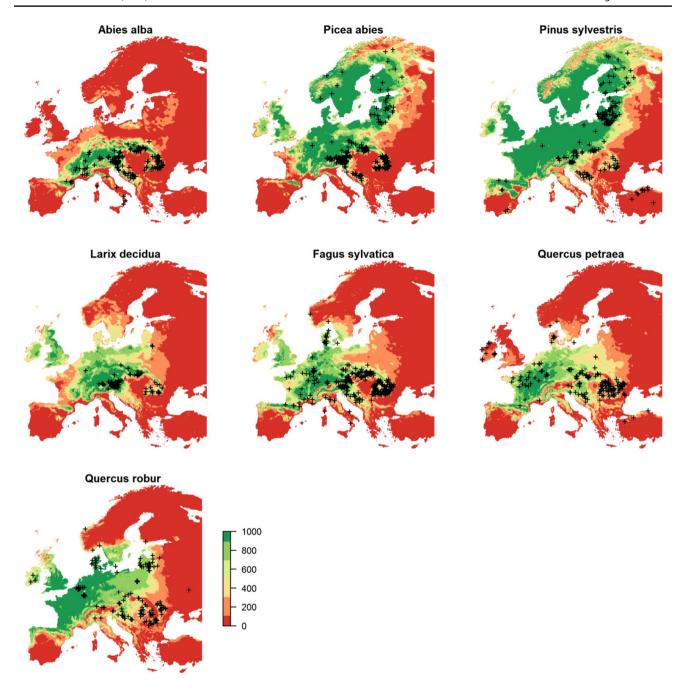


Fig. 3 Locations of the genetic conservation units (Lefèvre et al. 2013) plotted against the predictions of the ensemble SDMs for the period 1961-1990 for the seven target species of Europe. The prediction range 0-1000 refers to 0-100%

Table 5 Statistics for evaluation for each of the models used to develop the ensemble SDM for the seven tree species.

The summary of this model evaluation is presented in Table 1

Criteria	Testing data	Evaluating data	Sensitivity	Specificity	Model	Species
TSS	0.921	0.916	96.718	94.925	GLM	Abies alba
ROC	0.99	0.99	96.334	95.522	GLM	Abies alba
TSS	0.936	0.933	96.377	96.887	GBM	Abies alba
ROC	0.995	0.994	96.377	96.972	GBM	Abies alba
TSS	0.949	0.939	97.357	96.588	GAM	Abies alba
ROC	0.996	0.995	96.121	98.038	GAM	Abies alba
TSS	0.936	0.932	95.396	97.825	CTA	Abies alba
ROC	0.978	0.977	95.78	97.612	CTA	Abies alba
TSS	0.962	0.956	97.4	98.209	ANN	Abies alba
ROC	0.993	0.992	97.144	98.806	ANN	Abies alba
TSS	0.743	0.745	79.199	95.309	SRE	Abies alba
ROC	0.872	0.873	79.199	95.309	SRE	Abies alba
TSS	0.927	0.92	96.633	95.394	FDA	Abies alba
ROC	0.987	0.987	95.951	96.418	FDA	Abies alba
TSS	0.929	0.927	96.292	96.418	MARS	Abies alba
ROC	0.992	0.992	96.377	96.375	MARS	Abies alba
TSS	0.998	0.968	98.167	98.635	RF	Abies alba
ROC	1.00	0.998	98.679	98.337	RF	Abies alba
TSS	0.872	0.884	94.246	94.2	MAXENT*	Abies alba
ROC	0.979	0.981	95.482	93.262	MAXENT*	Abies alba
TSS	0.802	0.804	93.126	87.25	GLM	Fagus sylvatica
ROC	0.956	0.955	93.081	87.305	GLM	Fagus sylvatica
TSS	0.825	0.818	92.991	88.806	GBM	Fagus sylvatica
ROC	0.971	0.97	93.723	88.25	GBM	Fagus sylvatica
TSS	0.826	0.827	94.375	88.384	GAM	Fagus sylvatica
ROC	0.820	0.969	94.263	88.517	GAM	Fagus sylvatica
TSS	0.859	0.85	93.543	91.441	CTA	= -
ROC	0.859	0.959	93.543	91.441	CTA	Fagus sylvatica Fagus sylvatica
TSS	0.849	0.846	93.993	90.585	ANN	Fagus sylvatica
ROC	0.849	0.971	95.106	89.595	ANN	•
TSS	0.6	0.586		83.337	SRE	Fagus sylvatica
ROC	0.8		75.307 75.307	83.337	SRE	Fagus sylvatica Fagus sylvatica
TSS	0.794	0.793 0.793	75.307 90.899	88.395	FDA	0 ,
						Fagus sylvatica
ROC	0.958	0.958	92.598	86.972	FDA	Fagus sylvatica
TSS	0.811	0.809	92.789	88.072	MARS	Fagus sylvatica
ROC	0.961	0.961	92.238	88.751	MARS	Fagus sylvatica
TSS	0.994	0.935	97.278	96.187	RF	Fagus sylvatica
ROC	1	0.994	97.188	96.343	RF	Fagus sylvatica
TSS	0.755	0.752	93.61	81.525	MAXENT*	Fagus sylvatica
ROC	0.926	0.927	93.835	81.381	MAXENT*	Fagus sylvatica
TSS	0.858	0.867	95.254	91.423	GLM	Larix decidua
ROC	0.975	0.976	95.548	91.277	GLM	Larix decidua
TSS	0.894	0.891	94.765	94.201	GBM	Larix decidua
ROC	0.987	0.985	94.716	94.591	GBM	Larix decidua
TSS	0.91	0.911	96.282	94.786	GAM	Larix decidua
ROC	0.988	0.987	95.89	95.224	GAM	Larix decidua
TSS	0.92	0.906	96.233	94.396	CTA	Larix decidua
ROC	0.978	0.973	96.233	94.396	CTA	Larix decidua
TSS	0.924	0.923	96.722	95.614	ANN	Larix decidua
ROC	0.991	0.989	95.841	96.686	ANN	Larix decidua
TSS	0.656	0.651	77.153	87.914	SRE	Larix decidua



 Table 5 (continued)

Criteria	Testing data	Evaluating data	Sonoitivity	Specificity	Model	Species
		Evaluating data	Sensitivity	Specificity		Species
ROC	0.828	0.825	77.153	87.914	SRE	Larix decidua
TSS	0.863	0.871	95.548	91.52	FDA	Larix decidua
ROC	0.974	0.974	95.303	92.251	FDA	Larix decidua
TSS	0.878	0.888	96.526	92.3	MARS	Larix decidua
ROC	0.981	0.98	96.575	92.3	MARS	Larix decidua
TSS	0.997	0.96	98.386	97.661	RF	Larix decidua
ROC	1	0.996	98.337	97.758	RF	Larix decidua
TSS	0.735	0.754	95.01	80.361	MAXENT*	Larix decidua
ROC	0.917	0.924	95.01	80.409	MAXENT*	Larix decidua
TSS	0.834	0.834	91.633	91.827	GLM	Pice abies
ROC	0.975	0.975	91.93	91.58	GLM	Pice abies
TSS	0.895	0.898	96.673	93.09	GBM	Pice abies
ROC	0.986	0.987	96.615	93.192	GBM	Pice abies
TSS	0.893	0.897	95.143	94.591	GAM	Pice abies
ROC	0.987	0.987	94.692	95.171	GAM	Pice abies
TSS	0.921	0.917	97.631	94.028	CTA	Pice abies
ROC	0.979	0.978	97.631	94.028	CTA	Pice abies
TSS	0.875	0.873	96.393	90.915	ANN	Pice abies
ROC	0.965	0.965	96.484	90.889	ANN	Pice abies
TSS	0.643	0.643	75.589	88.662	SRE	Pice abies
ROC	0.821	0.821	75.589	88.662	SRE	Pice abies
TSS	0.829	0.832	91.553	91.648	FDA	Pice abies
ROC	0.974	0.975	93.334	90.104	FDA	Pice abies
TSS	0.861	0.865	93.419	93.073	MARS	Pice abies
ROC	0.979	0.98	94.35	92.228	MARS	Pice abies
TSS	0.998	0.985	99.515	98.968	RF	Pice abies
ROC	1	0.998	99.538	98.968	RF	Pice abies
TSS	0.606	0.604	94.019	66.362	MAXENT*	Pice abies
ROC	0.88	0.88	94.492	65.953	MAXENT*	Pice abies
TSS	0.787	0.789	91.278	87.63	GLM	Pinus sylvestris
ROC	0.958	0.958	91.74	87.281	GLM	Pinus sylvestris
TSS	0.872	0.864	96.999	89.344	GBM	Pinus sylvestris
ROC	0.976	0.974	94.859	91.808	GBM	Pinus sylvestris
TSS	0.857	0.859	94.526	91.366	GAM	-
ROC	0.837	0.839	93.778	92.26	GAM	Pinus sylvestris Pinus sylvestris
TSS	0.970	0.9	97.731	92.249	CTA	Pinus sylvestris
ROC	0.968	0.964	97.731	92.362	CTA	Pinus sylvestris
			96.08			Pinus sylvestris
TSS	0.886	0.886 0.964		92.537	ANN ANN	•
ROC	0.966		95.789	92.875		Pinus sylvestris
TSS	0.572	0.579	76.21	81.686	SRE	Pinus sylvestris
ROC	0.786	0.789	76.21	81.686	SRE	Pinus sylvestris
TSS	0.803	0.802	91.638	88.533	FDA	Pinus sylvestris
ROC	0.961	0.96	93.009	87.517	FDA	Pinus sylvestris
TSS	0.829	0.831	95.176	87.917	MARS	Pinus sylvestris
ROC	0.966	0.966	94.628	88.584	MARS	Pinus sylvestris
TSS	0.998	0.975	99.048	98.47	RF	Pinus sylvestris
ROC	1	0.997	99.145	98.44	RF	Pinus sylvestris
TSS	0.503	0.506	93.101	57.479	MAXENT*	Pinus sylvestris
ROC	0.819	0.816	93.413	57.243	MAXENT*	Pinus sylvestris
TSS	0.849	0.851	91.782	93.277	GLM	Quercus robur
ROC	0.976	0.977	91.73	93.418	GLM	Quercus robur



 Table 5 (continued)

Criteria	Testing data	Evaluating data	Sensitivity	Specificity	Model	Species
TSS	0.889	0.892	96.048	93.175	GBM	Quercus robur
ROC	0.985	0.986	94.818	94.517	GBM	Quercus robur
TSS	0.88	0.882	94.87	93.328	GAM	Quercus robur
ROC	0.983	0.984	95.342	92.97	GAM	Quercus robur
TSS	0.91	0.909	96.218	94.696	CTA	Quercus robur
ROC	0.977	0.978	96.218	94.696	CTA	Quercus robur
TSS	0.915	0.917	96.794	94.875	ANN	Quercus robur
ROC	0.984	0.984	96.336	95.386	ANN	Quercus robur
TSS	0.718	0.72	76.93	95.066	SRE	Quercus robur
ROC	0.859	0.86	76.93	95.066	SRE	Quercus robur
TSS	0.844	0.844	92.423	92.037	FDA	Quercus robur
ROC	0.974	0.977	92.044	92.523	FDA	Quercus robur
TSS	0.859	0.857	92.58	93.175	MARS	Quercus robur
ROC	0.977	0.979	92.306	93.494	MARS	Quercus robur
TSS	0.996	0.965	98.574	97.968	RF	Quercus robur
ROC	1	0.998	98.09	98.556	RF	Quercus robur
TSS	0.778	0.787	95.878	82.848	MAXENT*	Quercus robur
ROC	0.943	0.946	95.773	82.975	MAXENT*	Quercus robur
TSS	0.754	0.747	94.685	80.019	GLM	Quercus petraea
ROC	0.942	0.945	93.45	81.709	GLM	Quercus petraea
TSS	0.789	0.788	89.93	88.988	GBM	Quercus petraea
ROC	0.962	0.962	90.629	88.401	GBM	Quercus petraea
TSS	0.806	0.805	91.865	88.565	GAM	Quercus petraea
ROC	0.962	0.962	91.072	89.739	GAM	Quercus petraea
TSS	0.856	0.834	93.986	89.458	CTA	Quercus petraea
ROC	0.957	0.953	93.986	89.458	CTA	Quercus petraea
TSS	0.831	0.835	92.96	90.514	ANN	Quercus petraea
ROC	0.961	0.963	92.821	90.679	ANN	Quercus petraea
TSS	0.643	0.658	79.674	86.124	SRE	Quercus petraea
ROC	0.821	0.829	79.674	86.124	SRE	Quercus petraea
TSS	0.766	0.764	92.051	84.269	FDA	Quercus petraea
ROC	0.949	0.951	90.49	86.194	FDA	Quercus petraea
TSS	0.782	0.783	95.455	82.883	MARS	Quercus petraea
ROC	0.952	0.953	95.618	82.789	MARS	Quercus petraea
TSS	0.992	0.901	95.431	94.811	RF	Quercus petraea
ROC	1	0.989	95.501	94.811	RF	Quercus petraea
TSS	0.702	0.685	92.238	76.286	MAXENT*	Quercus petraea
ROC	0.9	0.898	94.126	74.618	MAXENT*	Quercus petraea

<sup>\*</sup>MAXENT Tsuruoka

**Table 6** Predicted probability of occurrence of the seven target species predicted for independent data of European genetic conservation units from Lefèvre et al. (2013). Probability class of 0–40, and 40–60 were

assumed to be incorrectly predicted and > 60% as correctly predicted by the SDMs

Probability class	Number of genetic conservation units in respective probability class							
	A alba	P abies	P sylvestris	L decidua	F sylvatica	Q petraea	Q robur	
0–40	4	1	17	2	5	26	23	
40-60	9	16	24	9	38	18	6	
60-80	32	34	18	6	96	95	62	
80-100	182	318	152	108	208	86	82	



**Acknowledgement** We acknowledge the cooperation of all participating institutes of the Interreg CE-SUSTREE project in compiling the dataset. We also acknowledge Dr. Laura Dobor and Dr. Tomáš Hlásny supported by the grant "EVA4.000, No. CZ.02.1.01/0.0/0.0/16\_019/0000803" financed by OP RDE for their contribution to acquiring the EURO-CORDEX climate data.

**Funding** The research was funded by INTERREG-Central Europe program (Project SUSTREE: Conservation and sustainable utilization of forest tree diversity in climate change).

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

### References

- Akaike H (1974) A new look at the statistical model identification. IEEE Trans Automat Control. https://doi.org/10.1109/TAC.1974.1100705
- Allen CD, Macalady AK, Chenchouni H et al (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manage 259:660–684. https://doi.org/10.1016/j.foreco.2009.09.001
- Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x
- Benito Garzón M, Alía R, Robson TM, Zavala MA (2011) Intra-specific variability and plasticity influence potential tree species distributions under climate change. Glob Ecol Biogeogr 20:766–778. https://doi.org/10.1111/j.1466-8238.2010.00646.x
- Booth GD, Niccolucci MJ, Schuster EG (1994) Identifying proxy sets in multiple linear-regression - an aid to better coefficient interpretation. USDA For Serv Intermt Res Stn Res Pap
- Breiman L (2001) Random forests. Mach Learn 45:5–32. https://doi. org/10.1023/A:1010933404324
- Chakraborty D, Schueler S, Lexer MJ, Wang T (2019) Genetic trials improve the transfer of Douglas-fir distribution models across continents. Ecography 42:88–101. https://doi.org/10.1111/ecog.03888
- Chakraborty D, Dobor L, Hlásny T, Schueler S (2020) High-resolution gridded climate data for Europe based on bias-corrected EURO-CORDEX: the ECLIPS-2.0 dataset [Zenodo: https://doi.org/10.5281/ zenodo.3952159]
- Chakraborty D, Móricz N, Rasztovits E, Dobor L, Schueler S (2020) Provisioning forest and conservation science with European tree species distribution models under climate change. V1. Zenodo. https://doi.org/10.5281/zenodo.3686918
- Coetzee BWT, Robertson MP, Erasmus BFN et al (2009) Ensemble models predict important bird areas in southern Africa will become less effective for conserving endemic birds under climate change. Glob Ecol Biogeogr 18:701–710. https://doi.org/10.1111/j. 1466-8238.2009.00485.x
- Craney TA, Surles JG (2002) Model-dependent variance inflation factor cutoff values. Qual Eng 14(3):391–403. https://doi.org/10.1081/QEN-120001878

- Dyderski MK, Paź S, Frelich LE, Jagodziński AM (2018) How much does climate change threaten European forest tree species distributions? Glob Chang Biol 24:1150–1163. https://doi.org/10.1111/gcb.13925
- European Environmental Agency (2006) European forest types—the European forest types—categories and types for sustainable forest management reporting and policy. EEA technical report No 9/2006. ISBN: 2–9167–886–4
- Garate-Escamilla H, Hampe A, Vizcaino-Palomar N et al (2019) Rangewide variation in local adaptation and phenotypic plasticity of fitness-related traits in Fagus sylvatica and their implications under climate change. bioRxiv 513515. https://doi.org/10.1101/513515
- Giorgi F, Jones C, Asrar GR (2009) Addressing climate information needs at the regional level: the CORDEX framework. World Meteorol Organ Bull 58:175–183. https://doi.org/10.1109/ICASSP. 2009.4960141
- Guisan A, Tingley R, Baumgartner JB et al (2013) Predicting species distributions for conservation decisions. Ecol Lett 16:1424–1435. https://doi.org/10.1111/ele.12189
- Hamann A, Aitken SN (2013) Conservation planning under climate change: accounting for adaptive potential and migration capacity in species distribution models. Divers Distrib 19:268–280. https://doi. org/10.1111/j.1472-4642.2012.00945.x
- Hanewinkel M, Cullmann DA, Schelhaas M-JJ et al (2013) Climate change may cause severe loss in the economic value of European forest land. Nat Clim Chang 3:203–207. https://doi.org/10.1038/nclimate1687
- Härtl FH, Barka I, Hahn WA et al (2016) Multifunctionality in European mountain forests an optimization under changing climatic conditions. Can J For Res 46:163–171. https://doi.org/10.1139/cifr-2015-0264
- Hiederer R , Houston Durrant T, Micheli E (2011) Evaluation of BioSoil demonstration project—soil data analysis.—Vol. 24729 of EUR—Scientific and Technical Research, Publications Office of the European Union.
- Houston Durrant T, San-Miguel-Ayanz J, Schulte E, Suarez Meyer A (2011) Evaluation of BioSoil demonstration project: forest biodiversity—analysis of biodiversity module, vol. 24777 of EUR—Scientific and Technical Research (Publications Office of the European Union, 2011).
- Jacob D, Petersen J, Eggert B et al (2014) EURO-CORDEX: New high-resolution climate change projections for European impact research. Reg Environ Chang. https://doi.org/10.1007/s10113-013-0499-2
- Kreyling J, Schmid S, Aas G (2015) Cold tolerance of tree species is related to the climate of their native ranges. J Biogeogr 42:156– 166. https://doi.org/10.1111/jbi.12411
- Lefèvre F, Koskela J, Hubert J et al (2013) Dynamic Conservation of Forest Genetic Resources in 33 European Countries. Conserv Biol. https://doi.org/10.1111/j.1523-1739.2012.01961.x
- Maroschek M, Seidl R, Netherer S, Lexer MJ (2009) Climate change impacts on goods and services of European mountain forests. Unasylva 60(231):76–80
- Mauri A, Strona G, San-Miguel-Ayanz J (2017) EU-Forest, a high-resolution tree occurrence dataset for Europe. Sci Data 4:1–8. https://doi.org/10.1038/sdata.2016.123
- Mcshea WJ (2014) What are the roles of species distribution models in conservation planning? Environ Conserv 41:93–96
- Mina M, Bugmann H, Cordonnier T et al (2017) Future ecosystem services from European mountain forests under climate change. J Appl Ecol 54:389–401. https://doi.org/10.1111/1365-2664.12772
- Moreno A, Hasenauer H (2016) Spatial downscaling of European climate data. Int J Climatol 36:1444–1458. https://doi.org/10.1002/joc.4436
- O'Neill GA, Hamann A, Wang T (2008) Accounting for population variation improves estimates of the impact of climate change on



- species' growth and distribution. J Appl Ecol. https://doi.org/10.1111/j.1365-2664.2008.01472.x
- Pontius RG, Parmentier B (2014) Recommendations for using the relative operating characteristic (ROC). Landsc Ecol 29:367–382. https://doi.org/10.1007/s10980-013-9984-8
- R Core Team (2016) R Core Team R. R A Lang Environ Stat Comput R Found Stat Comput, Vienna, Austria. https://www.R-project.org
- Ramirez-Villegas J, Jarvis A (2010) Downscaling global circulation model outputs: the Delta method. Policy Analalysis working paper 1. International centre for Tropical Agriculture available at http://ccafs-climate.org/downloads/docs/Downscaling-WP-01.pdf
- Reyer C, Lasch-Born P, Suckow F et al (2014) Projections of regional changes in forest net primary productivity for different tree species in Europe driven by climate change and carbon dioxide. Ann For Sci 71:211–225. https://doi.org/10.1007/s13595-013-0306-8
- Scheffers BR, De Meester L, Bridge TCL et al (2016) The broad footprint of climate change from genes to biomes to people. Science 354/6313, aaf7671 https://doi.org/10.1126/science.aaf7671
- Schueler S, Falk W, Koskela J et al (2014) Vulnerability of dynamic genetic conservation units of forest trees in Europe to climate change. Glob Chang Biol 20:1498–1511. https://doi.org/10.1111/gcb.12476
- Seidl R, Schelhaas MJ, Lexer MJ (2011) Unraveling the drivers of intensifying forest disturbance regimes in Europe. Glob Chang Biol 17:2842–2852. https://doi.org/10.1111/j.1365-2486.2011.02452.x
- Seidl R, Schelhaas MJ, Rammer W, Verkerk PJ (2014) Increasing forest disturbances in Europe and their impact on carbon storage. Nat Clim Chang 4:806–810. https://doi.org/10.1038/nclimate2318
- Senay SD, Worner SP, Ikeda T (2013) Novel three-step pseudo-absence selection technique for improved species distribution modelling. PLoS One 8:e71218. https://doi.org/10.1371/journal.pone.0071218
- Sykes MT, Prentice IC, Cramer W (1996) A bioclimatic model for the potential distributions of north European tree species under present and future climates. J Biogeogr 23:203–233

- Thompson CG, Kim RS, Aloe AM, Becker BJ (2017) Extracting the variance in flation factor and other multicollinearity diagnostics from typical regression results. Basic Appl Soc Psych. https://doi.org/10.1080/01973533.2016.1277529
- Thuiller W, Albert C, Araújo MB et al (2008) Predicting global change impacts on plant species' distributions: future challenges. Perspect Plant Ecol Evol Syst 9:137–152. https://doi.org/10.1016/j.ppees. 2007.09.004
- Thuiller W, Georges D, Engler R (2016) biomod2: Ensemble platform for species distribution modeling. R Packag version 2:r560
- Thurm EA, Hernandez L, Baltensweiler A et al (2018) Alternative tree species under climate warming in managed European forests. For Ecol Manage 430:485–497. https://doi.org/10.1016/j.foreco.2018.08.028
- Valladares F, Matesanz S, Guilhaumon F et al (2014) The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecol Lett 17:1351–1364. https://doi.org/10.1111/ele.12348
- van Vuuren DP, Edmonds J, Kainuma M et al (2011) The representative concentration pathways: an overview. Clim Change 109:5–31. https://doi.org/10.1007/s10584-011-0148-z
- Yang W, Andreasson J, Graham P, Olsson J (2010) Distribution based scaling to improve usability of RCM regional climate model projections for hydrological climate change impact studies. Hydrol Res 41:211–229. https://doi.org/10.2166/nh.2010.004
- Zimmermann NE, Edwards TC, Graham CH et al (2010) New trends in species distribution modelling. Ecography (Cop) 33:985–989. https://doi.org/10.1111/j.1600-0587.2010.06953.x
- Zurell D, Franklin J, König C et al (2020) A standard protocol for reporting species distribution models. Ecography 01 June 2020 https://doi.org/10.1111/ecog.04960

