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A framework for climate-resilient forest planning and restoration: advances linking species distribution modelling, genetic adaptation and future climate scenarios

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Introduction: Climate change is reshaping the distribution, resilience, and genetic pool of European forests, posing major challenges for long-term forest restoration and adaptive management. Addressing these challenges requires approaches that integrate species-level responses, intra-specific genetic differentiation, and uncertainty associated with future climate projections.

Methods: An integrated statistical modelling framework was developed and applied to support climate-informed forest planning across Spain. The framework was applied to 44 forest species, 12 of which were further analysed at the genetic-group level, resulting in a total of 49 genetic groups (93 taxa in total), representing Mediterranean, Atlantic, montane, and restricted-distribution taxa. Climatic predictors were derived from 10 CMIP6 Earth System Models under four Shared Socioeconomic Pathways and three future time horizons (2021–2050, 2041–2070, 2071–2,100). Climate data were statistically downscaled to 1 km² resolution using observations from more than 5,500 meteorological stations and topographic covariates. Species distribution models were calibrated using an ensemble of algorithms and evaluated with robust performance metrics. Uncertainty was explicitly quantified using the Percentage of Climate Models Predicting Suitability (PCM–PS), providing spatially consistent measures of agreement across climate projections.

Results: Projections indicate a biogeographical reorganisation of forest climatic suitability across the Iberian Peninsula. Temperate and montane species, such as *Fagus sylvatica*, *Abies alba*, and *Taxus baccata*, are projected to experience

widespread suitability contraction, whereas Mediterranean and drought-tolerant taxa, including *Quercus ilex* and *Pinus halepensis*, show persistence or expansion towards northern latitudes and higher elevations. Modelling at the genetic-group level improved spatial precision and identified climate-resilient refugia where specific lineages may persist despite overall species-level declines. Under the high-emission SSP3-7.0 scenario, approximately 78% of species and 73% of genetic groups exhibit contraction trends.

Conclusion: By integrating species-level responses, genetic differentiation, climate projections, and explicit uncertainty analysis, this framework translates complex modelling outputs into decision-ready information for forest restoration and management. The results underscore the importance of local adaptive provenance transfer and multi-scenario planning to enhance forest resilience under climate change. Overall, the framework offers a replicable approach for evidence-based adaptation planning in forest ecosystems of southern Europe.

KEYWORDS

adaptive forest planning, climate change, climate uncertainty, forest restoration, genetic provenance groups, species distribution modelling

Introduction

Climate change is accelerating shifts in the distribution, structure, and resilience of forest ecosystems across Europe, posing profound challenges for ecological restoration, biodiversity conservation, and sustainable forest planning (Lindner et al., 2010; Seidl et al., 2017; IPCC, 2023). In the Iberian Peninsula—recognised as one of Europe's major biodiversity hotspots and a centre of endemism, where biogeographical contrasts, climatic gradients, and millennia of land use intersect—faces particularly complex and spatially heterogeneous impacts (Rey Benayas and Scheiner, 2002; Aedo et al., 2013). Anticipating the responses of forest species to future conditions demands regionally adapted (Gil-Guirardo et al., 2022), forward-looking approaches that combine climatic, ecological, and genetic perspectives (Peñuelas et al., 2017).

The concept of climate-resilience in ecological conservation and restoration has gained increasing attention over the past decade, emphasising the need to incorporate future climate projections into species selection, seed sourcing, and forest landscape design (Stein et al., 2014). Yet, most restoration strategies still rely on static assumptions about species' climatic tolerances or broad provenance zones—approaches that may prove unsuitable under future scenarios (Kübler and Günter, 2024; but see Carrillo-García et al., 2023). This mismatch between ecological dynamics and management practices can lead to maladaptation, threatening the persistence of both planted and natural forests (Potter and Hargrove, 2012; Magnan et al., 2016; Łabiszak and Wachowiak, 2025).

Species distribution models (SDMs) provide a robust and scalable framework to estimate suitability for species under alternative climate scenarios (Beaumont et al., 2005; Allouche et al., 2006; Guisan et al., 2017; Wang et al., 2016). When combined with high-resolution climate data, SDMs enable detailed assessments of potential range shifts, habitat stability, and climate-driven risks (Fick and Hijmans, 2017).

High-resolution and ecologically meaningful climate data are a critical prerequisite for robust species distribution modelling (Bedia et al., 2013), particularly in topographically complex regions such as the Iberian Peninsula (Romo et al., 2023; Goicolea et al., 2025; Goicolea et al., 2026). Coarse-resolution outputs from global climate

models often fail to capture local climatic gradients driven by elevation, exposure, and mesoscale atmospheric processes, limiting their usefulness for regional ecological applications (Guisan et al., 2025). Statistical downscaling approaches address these limitations by refining large-scale climate projections using local observations and topographic information, thereby improving spatial coherence and regional reliability (Mateo et al., 2019a, 2019b). In this context, climate projections derived from the latest generation of Earth System Models participating in CMIP6 provide a physically consistent basis for exploring future climate trajectories across alternative socio-economic pathways. When combined with regionally calibrated downscaling methodologies, these projections yield climate surfaces that better represent species–climate relationships, particularly in mountainous and transitional environments where local variability strongly conditions ecological responses (Mateo et al., 2019a).

Integrating climatic modelling with genetic differentiation adds an essential layer of ecological robustness, allowing the identification of intra-specific units with distinct adaptive capacities (Benito Garzón et al., 2019; Ameztegui et al., 2024). This perspective is particularly relevant for forest reproductive material (FRM) management, since provenance groups often exhibit heterogeneous responses to temperature and precipitation regimes (Kapeller et al., 2012; Di Fabio et al., 2024; del García Barrio et al., 2025). The inclusion of genetic variation within modelling frameworks, therefore, represents a critical step towards more adaptive, evidence-based forest planning (Scherrer et al., 2021).

This study addresses these challenges by developing and applying an integrated modelling framework to assess the climatic suitability of 44 Iberian forest species, 12 of which are represented by distinct genetic groups, under locally downscaled future climate projections. While recent climate-informed forest planning approaches increasingly rely on species distribution models and climate projections, many remain limited by coarse-resolution data, single-model projections, or species-level analyses that overlook intra-specific genetic differentiation and uncertainty. The proposed framework here combines high-resolution climate data, ensemble modelling across multiple SSP scenarios and time horizons, and genetic differentiation to overcome these limitations. Its outputs are delivered through a public web-based viewer, providing spatially explicit maps, indicators, and

decision-support tools to support species and provenance selection, the design of resilient green infrastructure, and adaptive forest restoration strategies across Spain.

This study aims to develop a robust SDM-based methodological framework based for climate-resilient forest management, restoration, and conservation. The framework is designed to: (1) integrate the latest advances and diverse modelling approaches, (2) establish quality criteria for climate, occurrence data, (3) define ecological and conservation criteria for selecting species and locally adapted varieties, (4) explicitly address climatic uncertainty by incorporating multiple Earth System Models and Shared Socioeconomic Pathways (5) provide a method to synthesise information and (6) evaluate changes in suitability between periods. Developed within the ForesteCCo project, the framework is complemented by a publicly accessible web-based viewer designed to support decision-making in forest planning and restoration.

Data and methods

We first produced an integrated modelling workflow that was implemented in the ForesteCCo project (Figure 1). The workflow illustrates how species and genetic group data, high-resolution climate projections, ensemble species distribution modelling, and uncertainty analysis are combined to generate spatially explicit indicators of climatic suitability change. The individual steps of this workflow are described in detail in the sections below.

Species and genetic group selection

We modelled the climatic suitability of 44 forest species of ecological, silvicultural, and restoration relevance across mainland Spain and the Balearic Islands. The selection spans a broad ecological and biogeographical spectrum, covering Mediterranean, Atlantic, montane, as well as specific environments throughout the territory. The species selection was advised by Spanish forest management technicians, as these species are commonly used in ecological restoration and included in the national forest reproductive material catalogues.¹

Species were grouped into functional types reflecting their dominant biogeographical distributions (Appendix 1), namely (1) Mediterranean taxa (six species), including drought-tolerant broad-leaves such as *Quercus suber* and *Pinus halepensis*, which dominate the lowlands and southern and eastern landscapes; (2) Atlantic taxa, with only four species: *Castanea sativa*, *Fagus sylvatica*, *Betula pubescens* and *Alnus glutinosa*, representing mesic environments in northern Iberia and riparian systems; (3) Montane and subalpine taxa (23 species), including *Pinus uncinata*, *Pinus nigra*, *Abies alba* and *Taxus baccata*, among others, which characterise high-elevation forests in the Pyrenees, Cantabrian Mountains or Sierra Nevada; (4) Widespread taxa (nine species), such as *Pinus pinaster* and *Arbutus unedo*, or Mediterranean characteristic species as *Quercus ilex*; this group has a broad ecological amplitude and occurs across most of the Iberian Peninsula; and (5) Restricted distribution taxa, with two species (*Abies pinsapo* and *Quercus canariensis*), which are confined to specific

mountain systems or biogeographical enclaves in southern and western Iberia.

For 12 species belonging to the genera *Quercus*, *Pinus*, and *Fagus*, models were also developed for distinct ecological/genetic groups (49 groups in total). These groups were identified based on the official provenance regions of forest species in Spain (Alía et al., 2009) and complemented with population genetic information synthesised from published molecular marker studies (del García Barrio et al., 2025). The delimitation of provenance-based genetic groups relies primarily on analyses using commercially available SNP markers, which characterise genome-wide patterns of genetic structure and provenance differentiation (del García Barrio et al., 2025). These markers are predominantly neutral and are therefore intended to represent genetic structure rather than experimentally demonstrated local adaptation. This approach allowed the evaluation of intra-specific climatic responses, increasing the ecological realism of projections and providing practical guidance for provenance-based restoration planning (Appendix 2).

The distribution of some species and genetic groups is shown in Appendix 3, which illustrate different ecological and biogeographical patterns. These are (a) *Pinus halepensis*, widely distributed in Mediterranean lowlands with five genetic groups; (b) *Quercus faginea*, a widespread oak with four genetic groups; (c) *Quercus petraea*, restricted to northern and northeastern Iberia mountain areas, with three genetic groups; and (d) *Abies pinsapo*, a fir confined to southern Spain.

The presence data for each of the species, and its designation as a determined genetic group when applicable, have been obtained from the combination of the MFE50 (2015 version) with the corresponding maps of Provenance Regions of forest species in Spain (Alía et al., 2009). This combination provides us with a database of native populations, understanding this term as those populations that were mature stands in the middle of the previous century, according to information collected from the first forest map of Spain (Ceballos, 1966). To maintain consistency with the climate data, the species vector information was overlaid with a 1 × 1 km reference grid. Occurrences of each species and genetic group were assigned to grid cells using a centroid-based matching method, thereby minimising overestimation in marginal areas. This procedure implicitly ensured spatial filtering by retaining a maximum of one occurrence per taxon and grid cell. Consequently, the effective spatial filtering distance corresponds to the grid resolution (1 km), ensuring spatial independence of occurrence data and consistency across species, genetic groups, and environmental predictors. A total of 44 species and 49 genetic groups were included in the analysis, yielding 93 taxa *sensu lato*.

Climatic and environmental data

The environmental dataset employed in this study integrates bioclimatic and edaphic variables at medium spatial resolution, harmonised to a 1 × 1 km raster grid (EPSG:4326 WGS84) for consistency across all modelling steps.

The climate data were produced from daily observations, including accumulated 24-h precipitation from 5,577 stations and daily maximum and minimum temperatures from 2,515 stations. These stations belong to the Spanish Meteorological Agency and are distributed across mainland Spain and the Balearic Islands.

Future projections were developed using the FICLIMA statistical downscaling methodology (Ribalaygua et al., 2013). This

¹ https://www.miteco.gob.es/es/biodiversidad/temas/recursos-geneticos/geneticos-forestales/rgf_catalogo_materiales_base.html

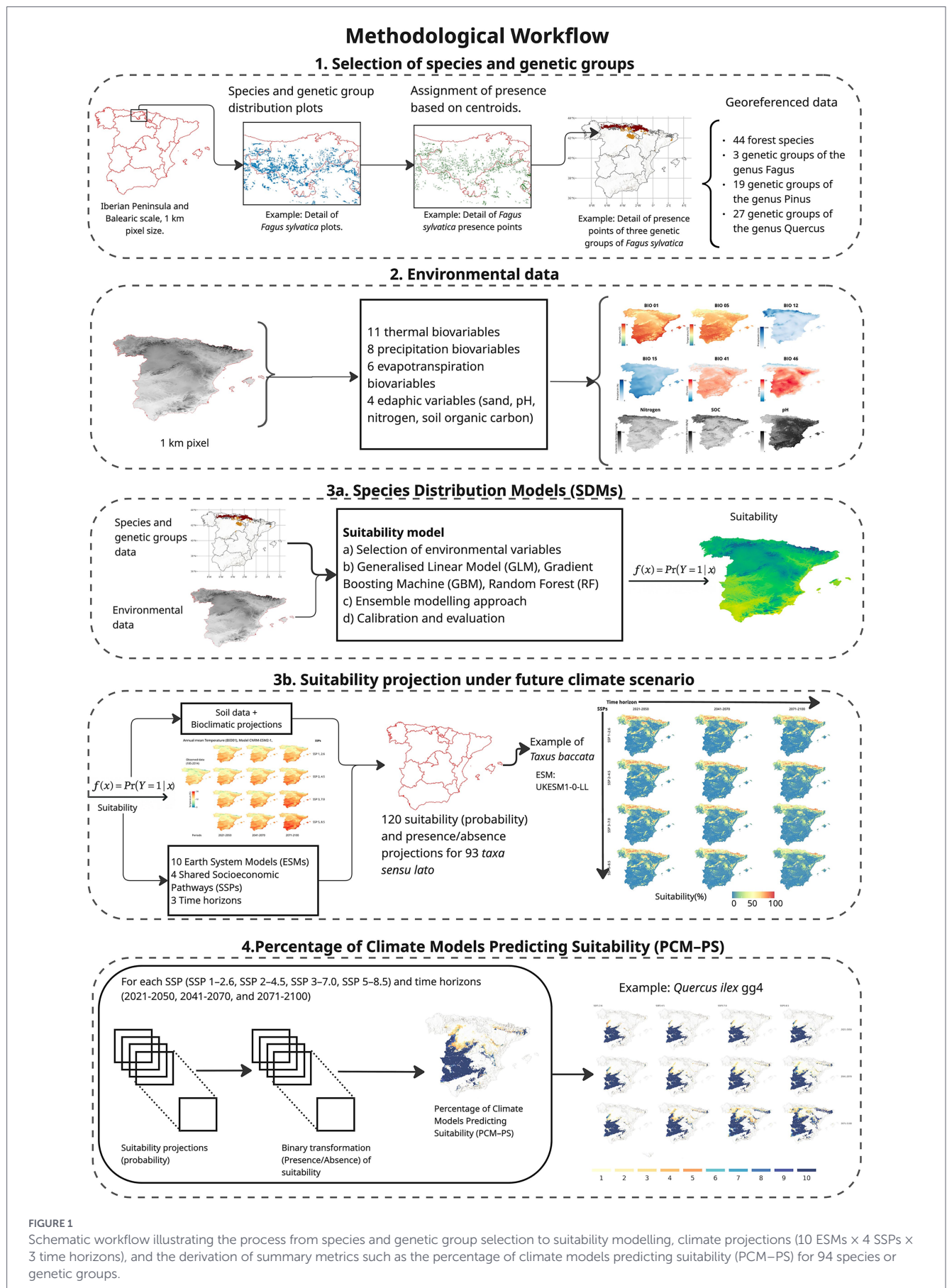


FIGURE 1

Schematic workflow illustrating the process from species and genetic group selection to suitability modelling, climate projections (10 ESMs $\times$ 4 SSPs $\times$ 3 time horizons), and the derivation of summary metrics such as the percentage of climate models predicting suitability (PCM-PS) for 94 species or genetic groups.

TABLE 1 CMIP6 earth system models (ESMs) used in the study, their native spatial resolution, and responsible centres.

CMIP6 model	Spatial resolution (lat × lon)	Responsible centre
ACCESS-CM2	1.258° × 1.8758°	Australian Community Climate and Earth System Simulator (ACCESS), Australia
BCC-CSM2-MR	1.125° × 1.121°	Beijing Climate Center (BCC), China Meteorological Administration, China
CanESM5	2.812° × 2.790°	Canadian Centre for Climate Modelling and Analysis (CCCma), Canada
CMCC-ESM2	1.25° × 0.942°	Euro-Mediterranean Center on Climate Change (CMCC), Italy
CNRM-ESM2-1	1.406° × 1.401°	National Centre for Meteorological Research (CNRM), Météo-France, France
EC-EARTH3	0.703° × 0.702°	EC-EARTH Consortium, Europe
MPI-ESM1-2-HR	0.938° × 0.935°	Max Planck Institute for Meteorology (MPI-M), Germany
MRI-ESM2-0	1.125° × 1.121°	Meteorological Research Institute (MRI), Japan
NorESM2-MM	1.250° × 0.942°	Norwegian Climate Centre (NCC), Norway
UKESM1-0-LL	1.875° × 1.250°	UK Met Office, Hadley Centre, United Kingdom

methodology follows a two-step process combining analogue stratification with regression and probabilistic techniques. Future projections were generated by downscaling the outputs of ten state-of-the-art Earth System Models (ESMs) participating in CMIP6, using the FICLIMA statistical methodology (Table 1). Model selection was guided by global coverage, performance, international recognition, and the availability of relevant variables.

The four Shared Socioeconomic Pathways (SSPs) recommended by the IPCC (2021a, 2021b) Sixth Assessment Report, which cover a wide spectrum of mitigation and development scenarios, were used: SSP1–2.6 (very optimistic), SSP2–4.5 (optimistic), SSP3–7.0 (pessimistic), and SSP5–8.5 (very pessimistic).

Thus, for each combination of model and SSP, downscaled daily series for each climate variable and each station were generated for the period 2015 to 2,100. Using these daily series—both observed and projected—30-year climatic averages were calculated for monthly precipitation (5,577 stations) and maximum and minimum temperatures (2,515 stations). These calculations were performed for the climate baseline (1985–2014) and for three projection horizons for each model and SSP, namely near-term (2021–2050), mid-century (2041–2070), and end-century (2071–2,100). All these climatic monthly averages were interpolated onto the 1 × 1 km grid using a multivariate thin plate spline (TPS) interpolation (Duchon, 1976), incorporating altitude, distance to the sea, longitude, latitude, and the orientation of mountain ranges as covariates. Thus, for the observed reference climate and for each combination of model, SSP, and time horizon—resulting in a total of 120 future climate scenarios— a set of 12 climatic monthly values (precipitation, maximum and minimum temperature) were produced for each 1 × 1 km grid cell.

From these climatic monthly sets, 25 bioclimatic variables were derived. The variables encompassed seasonal and annual metrics of temperature and precipitation, as well as reference evapotranspiration (ET_0). Nineteen of these variables correspond to those used by WorldClim (Fick and Hijmans, 2017), although some were adapted to address significant issues, particularly those related to the dry, wet, coldest, or warmest quarter. We detected that several original WorldClim variables—particularly those combining temperature and precipitation, such as BIO08 (mean temperature of the wettest quarter)—generated abrupt spatial discontinuities. These artefacts arise because the wettest quarter is dynamically defined and may correspond to different months across neighbouring cells. Small variations

in precipitation patterns, either spatially or between future horizons, can therefore shift the defining months and produce artificial jumps in temperature values unrelated to ecological processes. Similar discontinuities associated with dynamically defined bioclimatic variables have been documented by Booth (2022), who cautioned against their direct use in SDMs without prior verification. To avoid both spatial and temporal artefacts, we fixed the definition of the dry, wet, coldest, and warmest quarters based on the observed reference climate, applying these fixed definitions consistently across all grid cells and time periods. This procedure eliminated discontinuities and ensured a stable and ecologically interpretable set of bioclimatic predictors for modelling.

A custom ET_0 variable was developed to account for reductions in solar radiation exposure caused by topographic shading, thereby improving microclimatic precision in complex landscapes. In accordance with the WorldClim biovariables scheme, the values of ET_0 for the driest, wettest, coldest, and warmest months, and seasonality, were calculated. These ET_0 variables were calculated using the Penman-Monteith method (Allen et al., 1998), with solar radiation adjusted by a factor accounting the angle of solar incidence on the ground. This adjustment captures the effect of shade and sun exposure, which strongly influence vegetation dynamics.

To improve ecological robustness and model performance, four edaphic variables were included: sand content (g/kg), nitrogen (cg/kg), pH (×10), and soil organic carbon (dg/kg). All of these were obtained from the SoilGrids database² and referenced to the 0–5 cm soil depth (Poggio et al., 2021). The original 250-m resolution rasters were reprojected and resampled using bilinear interpolation to match the 1 × 1 km working grid. The final soil layers were aggregated into multiband raster cubes and subsequently integrated with the bioclimatic variables, resulting in a total of 29 predictors for the modelling process (Table 2). From the full set of 29 climatic and edaphic predictors used, nine representative variables are presented here to illustrate the diversity of environmental gradients across the Iberian Peninsula (Appendix 4).

Together, these climatic and environmental predictors capture the ecological diversity of the Iberian Peninsula, from humid Atlantic

² www.soilgrids.org

TABLE 2 Bioclimatic and environmental variables (BIO codes and soil parameters) used as predictors in the modelling framework.

Cod	Description
BIO01	Annual mean temperature (°C)
BIO02	Diurnal temperature range (monthly mean (max temp - min temp)) (°C)
BIO03	Isothermality: Relationship between the temperature range between day and night and between summer and winter (%)
BIO04	Seasonality in temperature (standard deviation*100)
BIO05	Maximum temperature of the warmest month (°C)
BIO06	Minimum temperature of the coldest month (°C)
BIO07	Annual temperature range (BIO05-BIO06) (°C)
BIO08	Average temperature of the wet quarter (°C)
BIO09	Average temperature of the dry quarter (°C)
BIO10	Average temperature of the warmest quarter (°C)
BIO11	Average temperature of the coldest quarter (°C)
BIO12	Annual precipitation (mm)
BIO13	Precipitation of the wettest month (mm)
BIO14	Precipitation of the driest month (mm)
BIO15	Seasonality in precipitation (Coefficient of variation) (%)
BIO16	Precipitation of the wettest quarter (mm)
BIO17	Precipitation of the driest quarter (mm)
BIO18	Precipitation of the hot quarter (mm)
BIO19	Precipitation of the coldest quarter (mm)
BIO41	Annual evapotranspiration (mm)
BIO42	Evapotranspiration of the driest month (mm)
BIO43	Evapotranspiration of the wettest or rainiest month (mm)
BIO44	Evapotranspiration of the warmest month (mm)
BIO45	Evapotranspiration of the coldest month (mm)
BIO46	Seasonality of evapotranspiration. Highest ETo - minimum Eto (mm)
SAND	Sand content (g/kg)
NIT	Nitrogen content (cg/kg)
SOC	Soil Organic Carbon (dg/kg)
pH	pH

forests to drought-prone Mediterranean systems, providing a robust baseline for modelling species suitability and genetic group responses under future climate scenarios.

Modelling methodology

Species distribution models (SDMs) were developed within an ensemble forecasting framework, designed to combine the predictive strengths of multiple algorithms and reduce model-specific biases (Araújo and New, 2007; Marmion et al., 2009; Mateo et al., 2019a; Mateo et al., 2024). All analyses were conducted in R (R Core Team, 2025) using the *covsel* package (Adde et al., 2023) for the variable selection and the *biomod2* package (Thuiller et al., 2023) for the implementation of the SDM.

Predictor selection followed a two-step embedded procedure

Predictor selection followed a two-step embedded procedure consisting of (a) Pairwise Pearson correlations ($|r| > 0.7$) to identify and iteratively remove highly collinear variables, retaining the most informative covariate in each correlated set; and (b) GLM with elastic-net penalties, GAM with null-space penalisation, and guided regularised Random Forest to rank covariates by importance across these models and select for final model calibration the top-ranked ones. This procedure aimed to enhance model interpretability and prevent redundancy and overfitting (Dormann et al., 2013; Adde et al., 2023).

Modelling calibration and algorithms

For each species and genetic group, models were then calibrated with three algorithms that have complementary strengths in ecological modelling: generalised linear models (GLM) (Guisan et al., 2002), random forests (RF) (Valavi et al., 2021), and boosted regression trees (BRT) (Elith et al., 2008). The joint use of these algorithms ensures the representation of both simple and complex ecological patterns, while reducing the influence of model specific assumptions and biases on the ensemble projections and ultimately increasing robustness and overall predictive accuracy (Araújo and New, 2007; Elith and Leathwick, 2009; Guisan et al., 2017; Mateo et al., 2024).

Pseudo-absence generation and model evaluation

A total of 10,000 pseudo-absence points were generated randomly throughout the study region except in cells of known presence (Barbet-Massin et al., 2012). During model calibration, pseudo-absences are weighted with a prevalence of 0.5, balancing their contribution relative to occurrences on the model fit regardless of their absolute number, thus preventing bias due to class imbalance. After assembling and weighting the occurrence–pseudo-absence dataset, the data were randomly split ten times into an 80% subset for model calibration and a 20% subset for evaluation following a cross-validation approach. Each algorithm (GLM, RF and BRT) was fitted with ten cross-validation replicates, resulting in 30 model runs for each species or genetic group. The model performance was assessed using the Area Under the Receiver Operating Characteristic Curve (AUC; Hanley and McNeil, 1982) and the True Skill Statistic (TSS; Allouche et al., 2006). These metrics collectively describe the discriminatory power, classification accuracy, and the reliability of suitability ranking. Replicates with AUC < 0.8 were excluded to ensure reliability (Araújo and New, 2007).

Ensemble modelling and thresholding

The consensus model for each taxon was then generated by averaging predictions from all retained replicates weighted by their AUC scores, thus favouring the most accurate replicates and reducing the influence of the less performant ones (Marmion et al., 2009). To evaluate the consensus model and to allow binarization, threshold values (cut-off) were determined by maximizing AUC criterion; the resulting thresholds were used to convert continuous suitability into binary presence–absence maps. This procedure generated an ensemble suitability map for the baseline climate period. As a result, three categories

of outputs were obtained: (1) statistical summaries synthesising model validity, (2) distribution maps of suitability for each taxon, and (3) potential presence/absence binary maps derived from optimal thresholds.

Projection to future climate scenarios

Finally, ensembled models were projected onto 120 future climate scenarios (ten GCMs $\times$ four SSPs $\times$ three projection horizons), yielding 120 suitability maps and 120 presence/absence maps per taxon.

Suitability shift analysis

The temporal dynamics of climatic suitability were assessed by comparing projections for the baseline period with those corresponding to each of the three future horizons (2021–2050, 2041–2070, and 2071–2,100) under the four SSPs. The analysis was carried out for each species and genetic group within the 1×1 km grid.

For each SSP-time horizon combination, suitability values were mapped for each of the 10 climate models individually, as well as summarised using for the median, the 25th percentile, and 75th percentile across models. This ensemble approach reduces biases of any single climate model. To assess the uncertainty among projections, the inter-quartile range was also computed.

PCM-PS (Percentage of Climate Models Predicting Presence) was applied to synthesise projections and quantify climate-model uncertainty. For each grid cell, SSP and time horizon, the PCM-PS was calculated. This index is defined as the proportion of climate models for which the SDMs, when forced with the climate of that model under the selected SSP and time horizon, predicted suitability above the binary threshold determined from the sensitivity-specificity maximisation criterion (Thuiller et al., 2009; Chacón-Moreno et al., 2025). PCM-PS values range from 0% (no climate model predicts suitability above the threshold) to 100% (all climate models predict suitability above the threshold). For the historical period (1985–2014), all models used the observed climate; therefore, values were categorised as 100% (if suitability exceeds the threshold under observed climate) or 0% (if it does not).

Accordingly, the complete set of 120 suitability layers (10 ESMs $\times$ 4 SSPs $\times$ 3 horizons) was integrated into a single PMCPs layer for each SSP and horizon, resulting in 12 ensemble maps per taxon. This methodological approach enabled a consistent and interpretable comparison of suitability patterns across space, scenarios, and time horizons, while reducing the influence of individual model biases (Guisan et al., 2017; Mateo et al., 2019a). In addition, evaluating agreement among climate models provides an explicit measure of the uncertainty associated with each SSP and projection period.

Synthesis of suitability change

From the full ensemble of model outputs —comprising 12 suitability maps per taxon (three projection periods across four SSPs in addition to the baseline map)— a synthesis analysis was conducted to summarise the temporal evolution of climatic suitability. Although the ForesteCCo modelling workflow generated a broader range of spatial and ecological indicators, the present

article focuses exclusively on changes in the total area of climatic suitability, used here as a synthetic measure of potential habitat dynamics.

For each species, the total suitable area in km² inferred from the number of pixels was calculated for the baseline period (1985–2014; central year $\approx$ 2000) and for three future horizons: 2021–2050 (centred on 2035), 2041–2070 (centred on 2055), and 2071–2,100 (centred on 2085). The synthesis presented in this study refers specifically to scenario SSP3–7.0, an intermediate-to-high forcing pathway that provides a consistent basis for cross-species comparison.

To enable the comparison of periods of unequal duration, a continuous rate of change was derived using an exponential-growth formulation:

$$r = \frac{\ln(A_t / A_{2000})}{t - 2000}$$

Where r represents the mean annual percentage rate of change and t is the midpoint year of each projection period (2035, 2055, 2085). This approach assumes a proportional, non-linear rate of change through time and allows direct comparison between expansion and contraction processes. Positive values of r indicate expansion of climatically suitable area, whereas negative values indicate contraction; the magnitude of r reflects the relative rate of change, allowing direct comparison across species and genetic groups.

Based on these results, a series of synthetic indicators was developed to describe the dominant climatic response of each species. First, the dominant trend provides an overall qualitative interpretation of the temporal trajectory of climatic suitability, distinguishing whether a species primarily exhibits contraction, expansion, persistence, or shift. Complementarily, the trend type characterises the shape and dynamics of the temporal response, differentiating between monotonic decline (a consistent decrease over time), accelerated decline (a rapid or non-linear reduction), and non-monotonic trajectories that involve transient recovery or stabilisation phases during the projection period.

Finally, the climate-change response category classifies the overall magnitude of change between the baseline and late-century horizons (centred on 2085), thereby providing a standardised measure of resilience or sensitivity. Species were considered highly resilient when the projected change was small ($-10\% \leq \Delta \leq +10\%$), moderately resilient for moderate losses ($-40\% < \Delta < -10\%$), vulnerable for marked declines ($-70\% < \Delta \leq -40\%$), and severely contracting when suitability decreased by more than 70% ($\Delta < -70\%$). Conversely, species showing gains $>30\%$ ($\Delta > +30\%$) were classified as expanding taxa or potential colonisers.

Spatial trends were identified through a visual interpretation of original suitability maps, which revealed the predominant directions and configurations of change in climatic suitability for each taxon.

Together, these indicators allow the comparison of species responses across a continuum of climatic pressures, linking the magnitude, direction, and temporal pattern of change within a single interpretative framework.

All spatial outputs generated within the ForesteCCo framework are accessible through a publicly available web-based viewer at: <https://forestecco.org>.

Results

Baseline and future climate patterns and environmental gradients

Temperature variables exhibit distinct latitudinal and altitudinal gradients. Mean annual temperature (BIO1) decreases toward northern and high-elevation regions, whereas the maximum temperature of August (BIO5) underscores the intense summer heat in southern and central Spain. Precipitation variables show an opposite trend, with annual precipitation (BIO12) highlighting the humid Atlantic fringe in the north and northwest. Precipitation seasonality (BIO15) reveals stronger seasonal contrasts in southern and eastern areas. Derived climatic indicators, such as annual reference evapotranspiration (BIO41) and its seasonality (BIO46), emphasize the Mediterranean water deficit, with highest values concentrated in eastern and southern regions and lowest values in montane and Atlantic-influenced zones. Edaphic predictors further illustrate forest heterogeneity. Soil nitrogen peaks in northern Atlantic areas and declines toward the interior plateau and Mediterranean lowlands. Soil organic carbon (SOC) follows a similar pattern, whereas soil pH shows the reverse, with acidic soils in the west and north and alkaline conditions dominating the Mediterranean basin (Appendix 4).

Related to future climate and as an illustrative example, Figure 2 shows projected changes in mean annual temperature (BIO1) using

the CNRM-ESM2-1 global climate model. The figure presents observed baseline conditions (1985–2014) alongside future projections for three time horizons (2021 to 2050, 2041 to 2070, and 2071 to 2,100) under four Shared Socioeconomic Pathways (SSP1–2.6, SSP2–4.5, SSP3–7.0, and SSP5–8.5). Although only one variable and one model are displayed here, the full dataset comprises 3,025 raster layers, covering 25 bioclimatic variables, 10 climate models, three time horizons, and four SSPs. These comprehensive climate layers provide the foundation for assessing species and genetic group suitability shifts under future conditions.

Species distribution modelling

The modelling framework yielded a large set of outputs describing the climatic suitability of forest species and their genetic groups under current and future conditions. The representative outputs are organised in three stages: model calibration and evaluation, projections under future climate scenarios, and synthesis products that integrate the main spatial and statistical patterns.

The calibration phase produced robust models across all taxa, as reflected in the statistical evaluation metrics (Table 3). The average AUC (ROC mean) values were consistently high, with relatively low variability among replicates, indicating stable discrimination between presences and absences. Similarly, the mean True Skill Statistic (TSS mean) exceeded accepted thresholds, with low standard deviations,

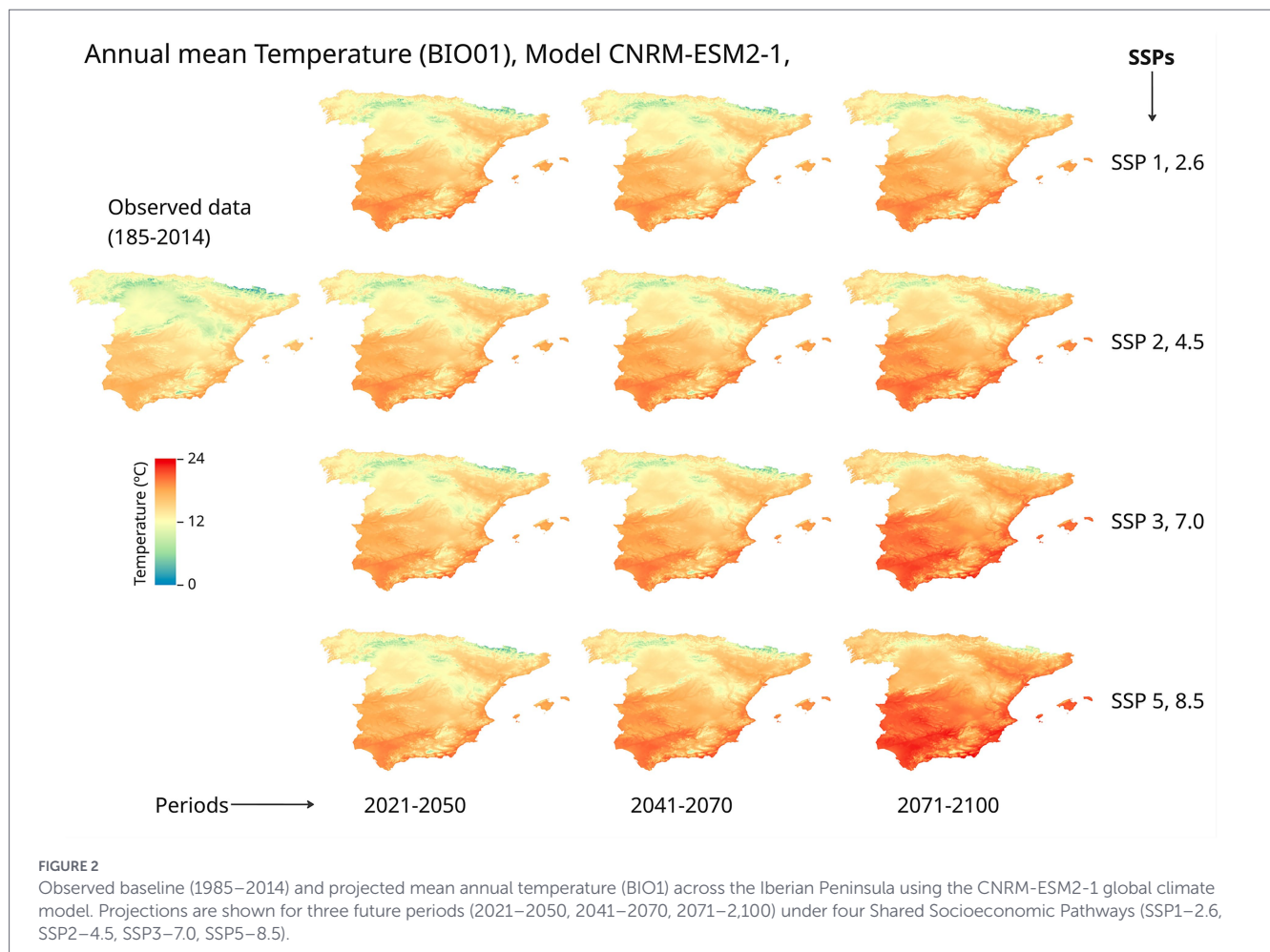


TABLE 3 Calibration and evaluation metrics of the baseline distribution models for the six selected species.

Species/ Genetic group	ROC	TSS	ROC-e	TSS-e	Threshold	Cal-p (n)	Unmod (%)	N° SV	SV	HI-v	I-v	MI-v
<i>Abies pinsapo</i>	0.999	0.654	1	1	0.74	32	0	8	BIO45 BIO03 BIO41 BIO12 BIO07 BIO17 Sand BIO06	BIO12 BIO07	BIO03	BIO45 BIO41
<i>Populus tremula</i>	0.942	0.689	0.983	0.851	0.52	593	10	9	BIO14 BIO41 BIO12 BIO45 BIO08 BIO07 BIO15 Sand BIO03	BIO08, BIO14, BIO12	BIO41	BIO03 BIO07
<i>F. sylvatica</i> , Galicia (GG1)	0.98	0.91	0.997	0.94	0.61	5,011	2	8	BIO01 BIO02 BIO13 BIO14 BIO43 Sand BIO15 BIO03	BIO14	BIO01 BIO02 BIO15	BIO13
<i>F. sylvatica</i> , Pyrenees (GG2)	0.989	0.93	0.999	0.959	0.66	1,533	2	9	BIO17 BIO12 BIO45 BIO41 BIO11 BIO02 Sand BIO15 BIO03	BIO11 BIO12	BIO17 BIO41	Sand BIO02
<i>P. pinea</i> , Northern Plateau (GG1)	0.984	0.913	0.998	0.962	0.59	1,343	1	8	BIO09 pH Sand BIO46 BIO43 BIO06 BIO15 BIO03	Sand pH	BIO09 BIO46	BIO15
<i>P. pinea</i> , Andalusia (GG3)	0.99	0.884	0.998	0.958	0.65	754	3	9	pH BIO04 BIO03 BIO45 BIO06 BIO15 BIO05 Sand BIO02	BIO15	BIO02 BIO03 BIO05	BIO06
<i>Q. ilex</i> , Eastern Sierra Morena– Alicante (GG2)	0.955	0.827	0.993	0.903	0.64	7,592	5	11	BIO01 BIO03 BIO04 BIO14 BIO15 Sand SOC BIO19 BIO41 BIO02 BIO45	BIO14	BIO02 BIO03 BIO15	BIO04 BIO41
<i>Q. ilex</i> , Balearic Islands (GG8)	0.998	0.986	1	0.997	0.81	1,020	0	9	BIO14 SOC BIO02 Sand BIO03 BIO15 BIO06 BIO19 BIO45	BIO15	BIO14	BIO06 Sand

ROC and TSS average, ROC-e and TSS-e average ensemble, Cal-p (n) is the number of calibration presences, Unmod (%) is unmodelled presence data, N° is number of selected variables, SV is the list of selected variables, HI-v is Highly important variables, I-v is important variables, and MI-v is moderated important variables.

confirming reliable classification performance. Presence data calibration confirmed that modelled suitability closely matched the observed distributions.

Variable importance analyses were conducted across model replicates to assess the relative contribution of climatic and edaphic predictors to species occurrences. A consistent subset of variables was repeatedly selected, enabling their classification into highly important, important, and moderately important predictors. Overall, temperature and water-related variables (including ET_0) emerged as dominant drivers of suitability, whereas soil properties provided additional explanatory value for specific taxa, notably *Abies pinsapo*. Together, these results demonstrate that the baseline models are both statistically reliable and ecologically coherent, providing a sound basis for subsequent projections under future climate scenarios.

The baseline models provide an accurate representation of the biogeographical patterns of Iberian forest species and genetic groups, offering insights into their current climatic suitability as a key component of their ecological niche and its relevance for management. Two species examples are presented in Figure 3. The model for *Abies pinsapo* captures its extremely restricted presence, confined to a few mountain enclaves in Grazalema Mountain Range, southern Spain. This narrow distribution highlights its vulnerability to climate change and the importance of targeted conservation actions. As a species with highly restricted distribution, it represents both a biogeographical relic and a flagship for Mediterranean montane conservation.

Populus tremula appears as a scattered but distinct element of Iberian mountain landscapes, with high suitability in the Pyrenees and other northern mountains. Its capacity for colonisation and clonal regeneration makes it ecologically important in dynamic forest mosaics. It also provides key habitat for associated biodiversity, especially in riparian and subalpine contexts.

Three species were selected to illustrate the results related to genetic groups: *Fagus sylvatica*, *Pinus pinea*, and *Quercus ilex* (Figure 4). These examples represent different biogeographical strategies, with *Fagus sylvatica* characterising Atlantic forests, *Pinus pinea* exemplifying Mediterranean taxa, and *Quercus ilex* illustrating a wide-spread species with multiple provenance regions across Iberia.

For each species, the modelled baseline climatic suitability of two representative genetic groups are shown, highlighting the spatial contrasts among them. For *Fagus sylvatica*, the Galicia (GG1) and Pyrenees (GG2) groups reflect adaptation to distinct Atlantic and montane environments. For *Pinus pinea*, groups from the Northern Plateau (GG1) and Andalusia (GG3) illustrate the species' ecological plasticity across continental and Mediterranean climates. For *Quercus ilex*, the comparison between Eastern Sierra Morena–Alicante (GG2) and the Balearic Islands (GG8) reveals marked differences between mainland and insular populations.

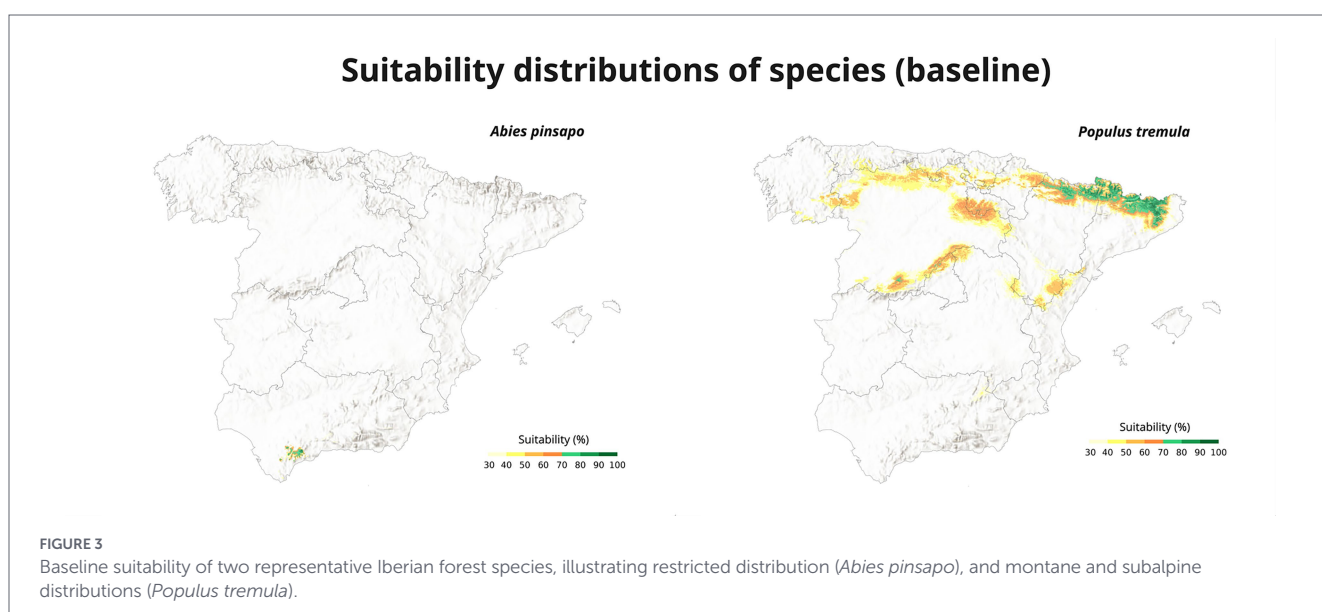
To provide a comprehensive context, the lower panels in the figure display the distribution of presence data for all genetic groups of each selected species, confirming the broad geographic differentiation and supporting the calibration of the models.

Analysis of suitability shift

To facilitate interpretation, the projections were synthesised into 12 maps per species or genetic group. Figure 5 illustrates the case of *Taxus baccata* and the genetic group *Quercus ilex* – Western (GG4). *T. baccata* shows a progressive reduction of suitable areas, tending towards disappearance under high-emission scenarios by the end of the century, whereas the *Quercus ilex* – Western genetic group 4 displays an expansion of suitability across the Iberian Peninsula.

The Percentage of Climate Models Predicting Suitability (PCM-PS) provides a reduced and internally consistent set of outputs that synthesise the full modelling framework, integrating both spatial patterns and area-based statistics. As an illustrative example, Figure 6 presents PCM-PS maps for *Arbutus unedo*, a species with a wide-spread distribution, and *Quercus canariensis*, which has a more restricted range, together with two genetic groups: *Pinus sylvestris* Eastern (GG3) and *Quercus ilex* Andalusia (GG1).

The comparison highlights contrasting patterns of stability, contraction, and potential expansion across taxa, reflecting differences between species with broad versus localised distributions, as well as between species-level and genetic group-level responses. For *Arbutus unedo* (Figure 6A), a progressive northward expansion of its potential distribution is observed, with an overall increase in climatically



suitable area over time, particularly under the more adverse climate scenarios. In contrast, *Quercus canariensis* (Figure 6B) appears to be highly favoured, especially across southern and eastern areas of the Iberian Peninsula and in the Balearic Islands. The two genetic groups (Figures 6C,D), however, show a consistent reduction in suitability across all scenarios and time horizons, with the Eastern genetic group of *Pinus sylvestris* disappearing entirely under the most severe scenario.

Dominant trends and response categories among forest taxa

As a result of the initial species-level analysis, it became evident that genetic groups (GGs) displayed more coherent and spatially consistent distribution patterns than species-level models alone. This reflects the refinement introduced by incorporating provenance-based genetic differentiation, which narrows ecological envelopes and reduces internal variability. Consequently, the synthesis integrates results from both species without defined genetic groups (32 taxa) and genetic groups (49 GGs), providing a comprehensive view of climatic suitability trends across organisational levels.

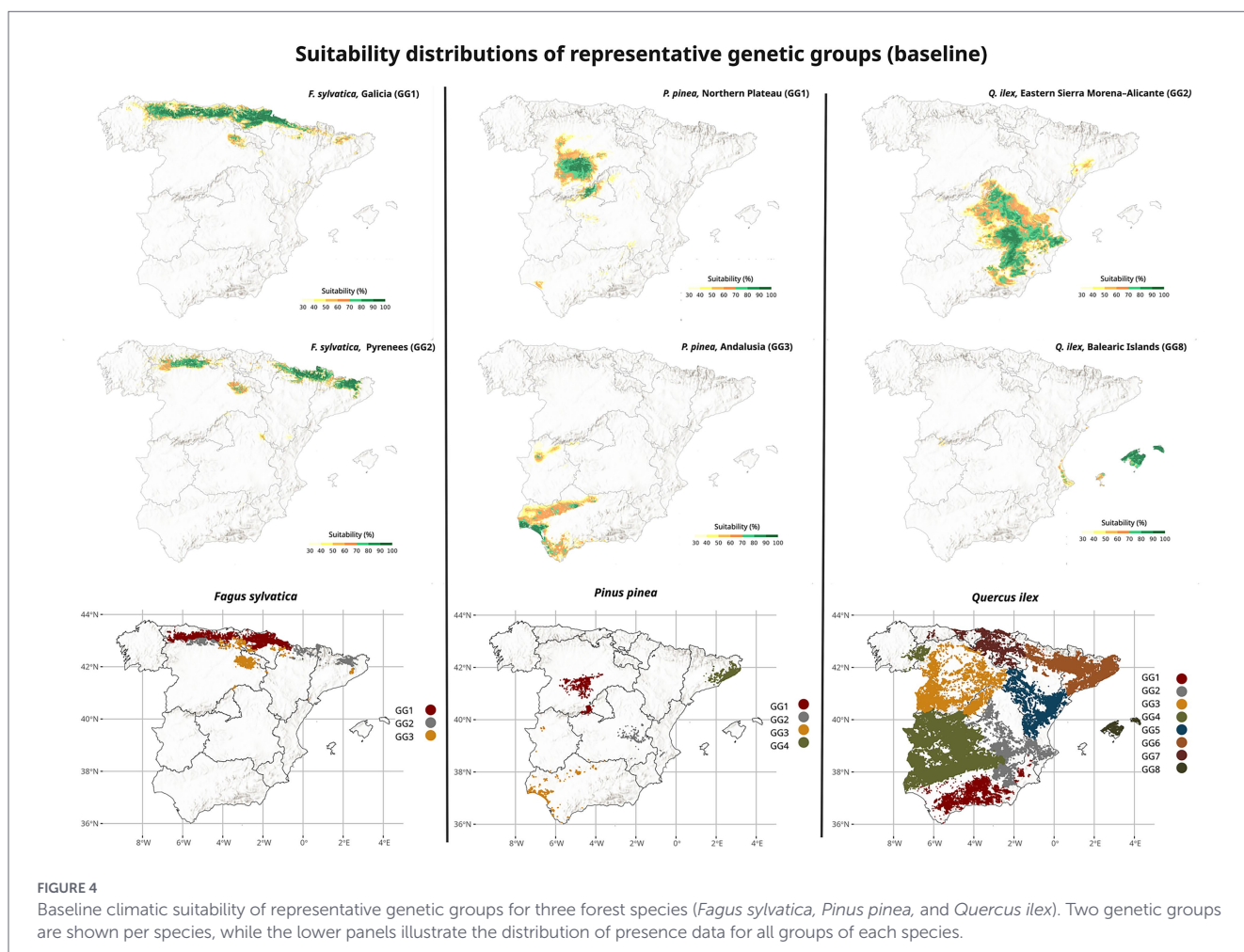
Based on the synthesis of projected suitable areas under scenario SSP3–7.0, taxa exhibited clear differences in their dominant climatic trajectories. The summary focuses on four categorical

indicators—Dominant trend, Trend type, Climate-change response category, and Spatial trend—with detailed numerical values provided in Appendix 5.

Regarding spatial trends, seven general response types were identified, capturing the principal spatial expressions of expansion, contraction, and persistence. (1) Upward shift reflects progressive displacement of suitable habitat towards higher elevations along mountain gradients. (2) Latitudinal expansion and (3) Westward expansion describe lateral redistributions towards higher latitudes or more oceanic regions. In contrast, (4) Lowland contraction denotes the loss of suitability at lower elevations without compensatory upslope gains. Some taxa exhibited (5) In-situ persistence, maintaining suitability within their current range, or (6) Local expansion, characterised by moderate gains without clear directional movement. At the opposite extreme, (7) In-situ disappearance indicates complete loss of suitability within the present range.

Species

The synthesis of species-level results (Table 4) reveals consistent patterns across dominant trends, temporal trajectories, and spatial responses. Some 78% of taxa (25 species) exhibit a contraction trend, primarily characterised by accelerated or monotonic declines in climatic suitability. Within this group, 10 species fall into the severely



contracting category, while nine are classified as moderately contracting category and one is classified as moderately resilient.

The spatial component of these contractions is largely associated with lowland contraction (14 cases) or upward shift along mountain gradients (9 cases), indicating a progressive loss of suitability at lower elevations and limited compensation upslope. A smaller subset (two taxa) shows *in situ* persistence, while a single case corresponds to *in situ* extinction, reflecting the complete loss of suitable habitat within the current range.

Six taxa (19%) display an expansion trend, showing either non-monotonic or strong exponential-like increases in suitability. These include species categorised as expanding (potential colonisers), with spatial patterns oriented towards higher latitudes, or westward expansion, depending on regional climatic influences.

Only one species —*Alnus glutinosa*— presents a pattern of persistence, defined by non-monotonic trajectories with transient recovery and classified as highly resilient, maintaining climatic suitability *in situ*. Overall, these results reflect the coexistence of contraction, persistence, and expansion responses, illustrating the diversity of potential adaptation pathways among Iberian forest taxa under future climatic conditions.

Genetic groups

The synthesis of results for genetic groups (GGs) (Table 5) shows a clear predominance of contraction trends, which account for more than 73% of all cases (36 GGs). Within this group, most

taxa exhibit accelerated declines in climatic suitability, leading to classification as severely contracting. The spatial component of these contractions is dominated by lowland contraction (23 cases), indicating a progressive loss of suitable habitats at the lower range margins without compensatory upslope expansion.

A smaller subset of contraction cases presents monotonic decline or non-monotonic trajectories with transient recovery, which are associated with vulnerable or moderately resilient responses. These GGs are distributed across both Mediterranean and montane environments, showing partial retention of suitable conditions at intermediate elevations.

In contrast, only four GGs show a persistence trend, characterised by non-monotonic or transient-recovery trajectories and classified as highly resilient. Their spatial behaviour includes *in situ* persistence, upward shift, lowland contraction, and westward expansion, suggesting that certain genetic lineages maintain stable or buffered microclimatic niches.

Expansion patterns are observed in nine GGs, reflecting non-monotonic stabilisation or strong exponential-like increases in climatic suitability. These expanding lineages are mostly classified as highly resilient or potential colonisers, with spatial patterns dominated by upward shifts and latitudinal expansion, and few cases of *in situ* persistence and local expansion.

Overall, the analysis indicates that, while contraction remains the prevailing trend among genetic groups, a limited subset (22%) exhibits persistence or even expansion, underscoring the heterogeneous adaptive potential of Iberian forest lineages under future climate scenarios.

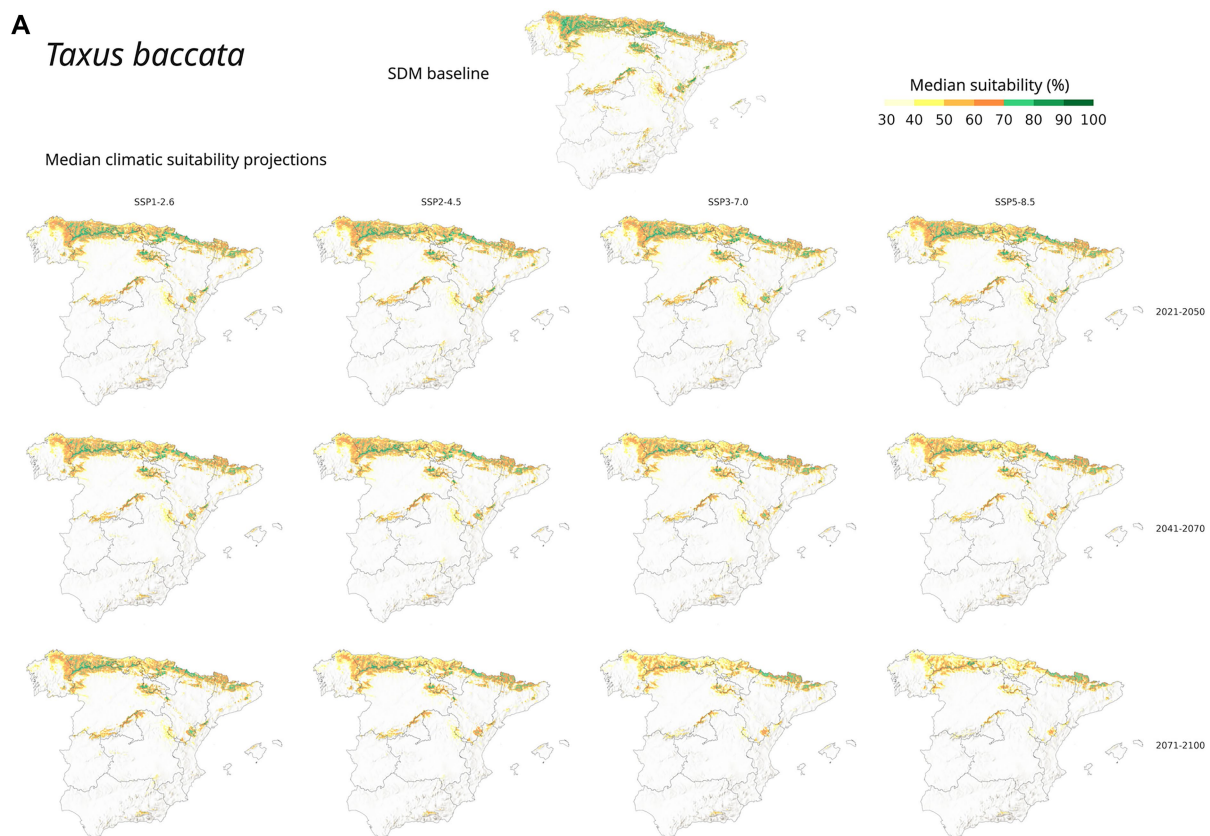


FIGURE 5 (Continued)

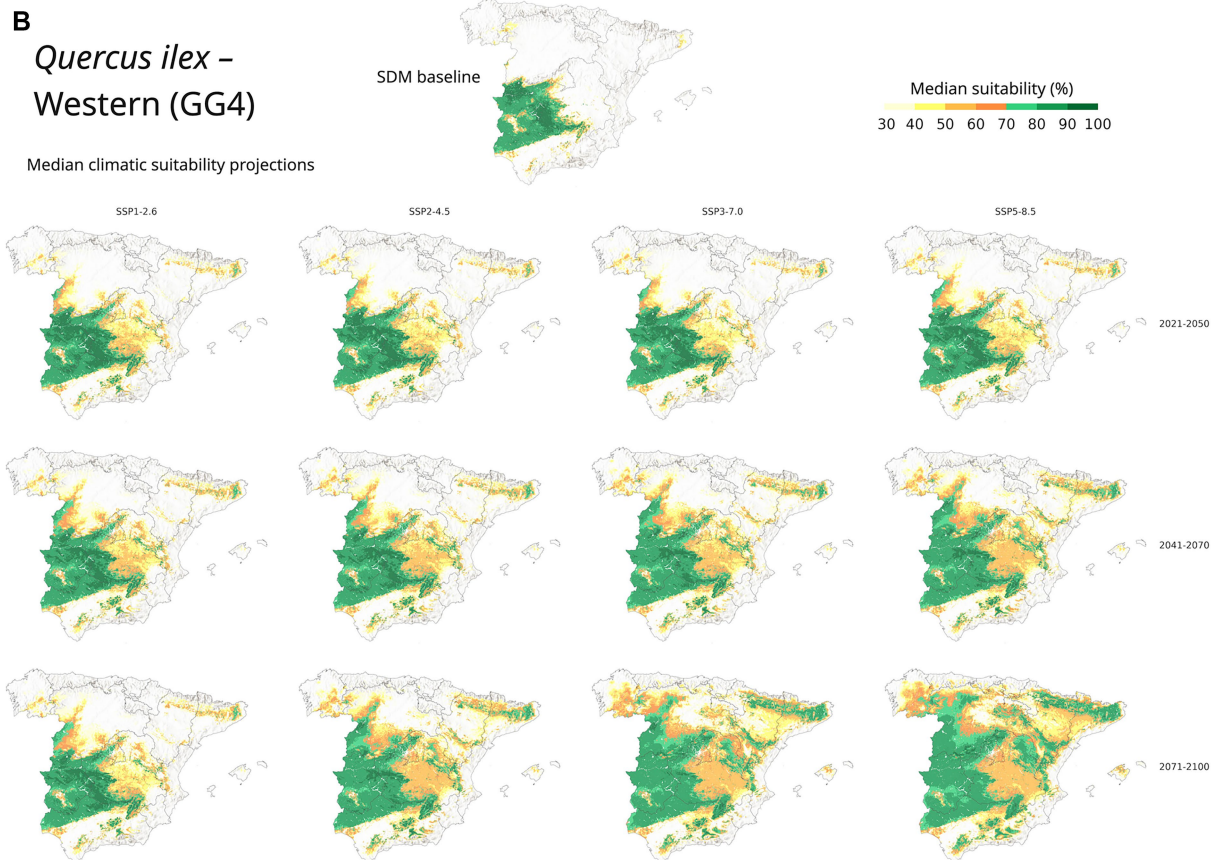


FIGURE 5

Baseline suitability model and median climatic suitability projections for (A) *Taxus baccata* and (B) genetic group *Quercus ilex* – western (GG4) under four SSP scenarios and three time horizons.

Discussion

The results presented here provide an integrated perspective on how climatic suitability for Iberian forest species—and, where relevant, their genetic groups—may change under future climate scenarios. By combining ensemble species distribution modelling, downscaled climate projections, and genetic-level stratification, this framework makes it possible to interpret suitability changes not only in terms of potential range shifts, but also in relation to local resilience and uncertainty. Beyond documenting spatial patterns of change, this approach supports a more operational interpretation of modelling outputs, linking projected suitability dynamics to practical decisions on species selection, seed sourcing, provenance deployment, and spatial prioritisation for restoration and climate adaptation. In the following sections, we discuss the methodological advances introduced by this framework, the main spatial patterns emerging from the results, and their implications for climate-resilient forest planning and restoration in Spain.

Integrative modelling framework and methodological advances

The ForesteCCo framework was designed as an integrative approach for climate-resilient forest planning, combining ensemble

Species Distribution Models (SDMs), locally downscaled climate projections, and provenance-based genetic information. This integration allows the assessment of climatic suitability for both forest species and genetic groups, while explicitly addressing future uncertainty through multi-model and multi-scenario analyses.

Recent national-scale initiatives have highlighted the importance of harmonising species occurrence data, environmental predictors, and SDM outputs into operational and transparent frameworks for biodiversity research and management. In this context, the geoSABINA platform provides a complementary example of how standardised spatial data and SDM products can support plant ecological research and conservation planning at broad scales (Goicolea et al., 2026). Building on similar principles, ForesteCCo extends this approach by explicitly incorporating future climate projections and genetic provenance information, thereby focusing on decision support for adaptive forest restoration.

Within this framework, three methodological components are particularly relevant: (i) species selection and distribution, (ii) ensemble SDM calibration and projection under future climate scenarios, and (iii) synthesis of suitability change and uncertainty using consensus-based metrics. Together, these components provide a coherent and transferable methodology for translating complex modelling outputs into decision-relevant information for forest planning.

i Species selection and distribution

The presence–absence database for each species and genetic group has two characteristics that confer particular robustness to the subsequent construction of the SDMs and their projections. First, it considers only natural populations, namely those mapped in the mid-twentieth century and identified as mature stands (Ceballos, 1966), which were subsequently verified and used in the delineation of Provenance Regions (Alía et al., 2009). Second, updating these stands using the Spanish National Forest Map (MFE50, 2015 version) allows the use of temporally stable presences (and absences in grid cells where the species is not recorded), thereby reinforcing the biogeographical basis required for SDM construction—namely, the assumption that species distributions are broadly in equilibrium with their climatic niche (see, e.g., Pulliam, 2000; Nogués-Bravo, 2009). This broad data foundation enhanced the capacity of the models to capture both regional and local climatic responses, an advantage consistent with the benefits of multi-scale SDMs that improve spatial accuracy by integrating broad climatic constraints with fine-scale habitat filters (Winiarski et al., 2025).

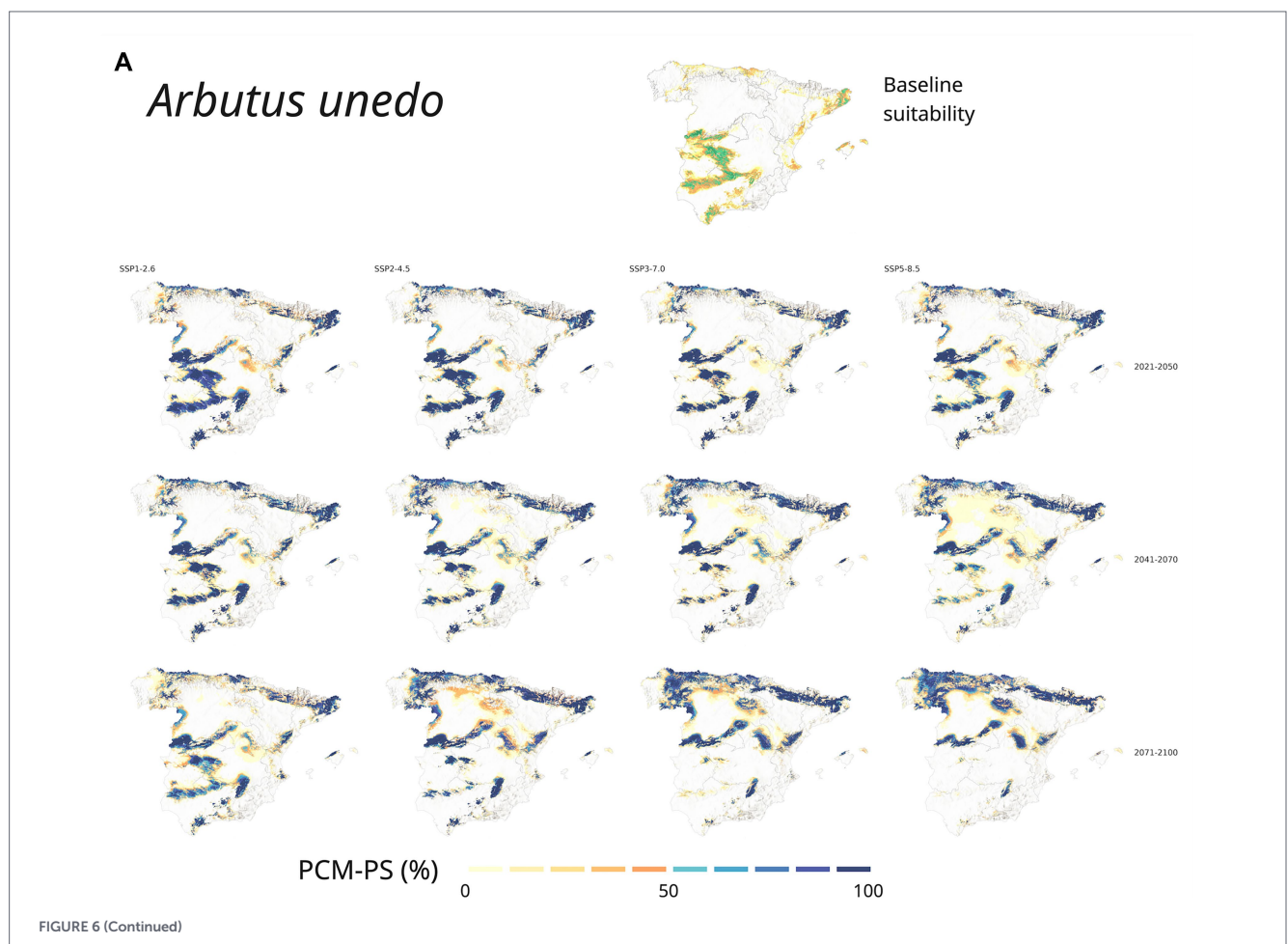
ii Species distribution modelling (SDMs)

A similar approach was applied by Mahmoud et al. (2024), who compared MaxEnt and an ensemble combining GLM, BRT, and RF to model Mediterranean native species in coastal Egypt. Their results showed high predictive accuracy and strong concordance between algorithms, confirming the value of combining multiple modelling

techniques and environmental variables to enhance robustness. This convergence supports the rationale of the ForesteCCo framework, where ensemble modelling and uncertainty assessment are central to building reliable, transferable projections for restoration and conservation planning. At broader spatial scales, complementary initiatives such as geoSABINA further illustrate the growing emphasis on harmonised SDM infrastructures and ensemble-based outputs to support applied biodiversity research and decision-making (Goicolea et al., 2026).

Model performance was evaluated with the True Skill Statistic (TSS), a prevalence-independent metric widely recommended for SDMs (Allouche et al., 2006). This evaluation confirmed that the improvements incorporated into the input variables lead to greater reliability of the SDMs. Among these improvements, it is worth mentioning the adaptations made to some WorldClim variables to avoid abrupt spatial and temporal discontinuities in their original formulation, the incorporation of high-resolution reference evapotranspiration variables that account for shade effects, and the integration of soil variables.

The value of consensus modelling for improving predictive reliability has also been demonstrated by Wang et al. (2016), who combined multiple SDM algorithms and climate projections to assess forest species responses across the Asia–Pacific region. Their ensemble approach reduced inter-model variability and produced coherent projections of range shifts, particularly for temperate and subtropical taxa. Similarly, Zou et al. (2025) showed that incorporating soil and



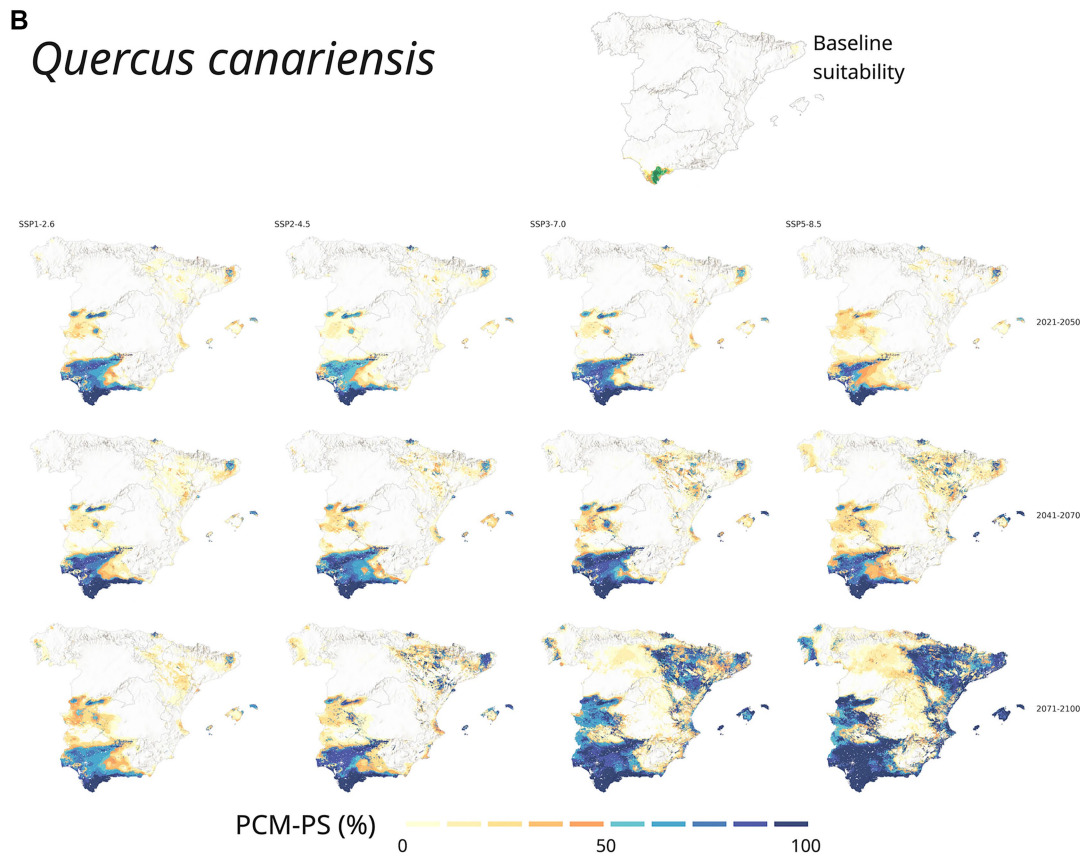


FIGURE 6 (Continued)

topographic variables alongside climatic predictors significantly improves spatial coherence and reduces uncertainty in Mediterranean forest projections. These findings parallel the rationale of ForesteCCo, where integrating diverse modelling techniques and synthesising uncertainty through consensus metrics such as PMC-PS strengthens both robustness and interpretability of suitability assessments.

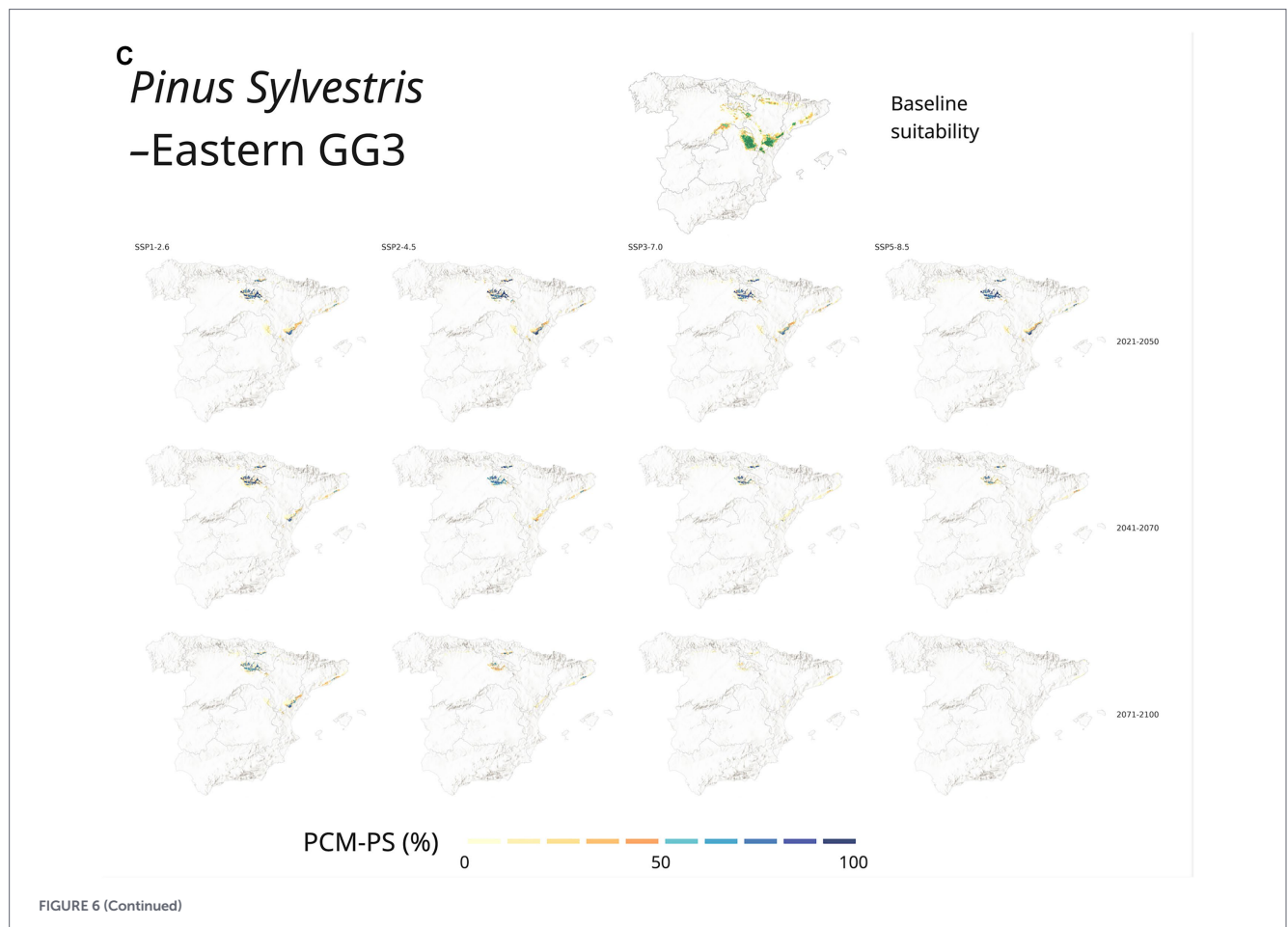
Furthermore, Sirén et al. (2025) highlighted that, while mechanistic or agent-based models may offer process-level detail, ensemble correlative approaches remain more transferable and practical for large-scale, multi-species applications. In this sense, the ensemble-based, data-driven design of ForesteCCo balances ecological realism and computational efficiency.

Finally, although ForesteCCo operates at a single spatial resolution (1 km), its hierarchical structure—integrating species- and genetic-group analyses across multiple time horizons—facilitates its potential linkage with landscape-level assessments of connectivity and resistance when combined with complementary spatial analyses. This interoperability—from taxon-level climatic suitability to broader spatial planning frameworks—reinforces the framework's capacity to inform adaptive restoration and climate-aware decision-making. The use of standardised bioclimatic predictors (Fick and Hijmans, 2017) further contributes to methodological consistency and transparency, enabling clearer interpretation of ensemble outputs and improving comparability with other modelling studies. By integrating ensemble modelling with both climatic and edaphic covariates, the framework provides operationally relevant projections that can support species and provenance selection under future climate scenarios.

iii Climate projections and uncertainty analysis

A key element underlying the robustness of the ForesteCCo framework is the use of state-of-the-art climate simulations and systematically downscaled datasets. All projections are based on CMIP6 Earth System Models (ESMs) and the Shared Socioeconomic Pathways (SSPs), which provide a physically consistent framework for exploring alternative future climate trajectories. To capture regional climatic nuances, these global simulations were downscaled and bias-corrected using the FICLIMA method, a statistically grounded approach that integrates local meteorological observations with topographic predictors to improve spatial coherence and regional reliability (Ribalaygua et al., 2013). This procedure reduces artefacts associated with coarse-resolution climate outputs, particularly in mountainous and coastal regions characterised by steep environmental gradients. The resulting bioclimatic variables, harmonised with the WorldClim 2 framework (Fick and Hijmans, 2017), provide a consistent 1 × 1 km gridded surface across Spain, enabling an ecologically meaningful representation of climatic heterogeneity. The use of multiple climate models and scenarios further strengthens the robustness of projections by capturing inter-model variability and supporting ensemble-based interpretations for adaptive forest planning.

A distinctive element of the methodology is the inclusion of 40 climate projections (10 models × 4 SSPs) and the use of percentile analysis (25th, 50th, and 75th) to explicitly represent the range of uncertainty associated with climate model simulations. Scenario construction and interpretation benefit from explicit analyses of



temperature and precipitation trajectories across time slices, sharpening the link between climatic drivers and projected suitability. It was therefore important to distinguish, at each spatial location, between models that consistently predict suitability and those that do not. For this purpose, we incorporated the Percentage of Climate Models Predicting Suitability (PMC–PS), which provides both an estimate of the viability of a species or genetic group under each SSP–time horizon and an explicit measure of uncertainty. Values close to 100% indicate strong agreement among all climate models and, therefore, lower uncertainty regarding future suitability, whereas values near 0% reflect strong agreement on future unsuitability.

Added value of genetic group modelling

Recent assessments of climate change impacts on Iberian forest species stress the need to incorporate genetic and provenance-based criteria into restoration planning (del García Barrio et al., 2025). Genetic diversity within species represents a fundamental resource for adaptation, supporting resilience through local adaptation, phenotypic plasticity, and selective processes under environmental change (Pakhira et al., 2024).

Moreover, vulnerability analyses based on geographically restricted datasets may underestimate the realised climatic niche of species, potentially biasing projections of future risk (Scherrer et al., 2021). Integrating genetic differentiation and provenance structure into modelling frameworks helps address these limitations and improves the ecological robustness of suitability assessments. Recognising and operationalising intra-specific diversity is therefore

central to climate-smart restoration, a core objective of the ForesteCCo framework.

Building on this rationale, Ameztegui et al. (2024) developed a quantitative approach for selecting provenances of *Pinus halepensis* suitable for reforestation under climate change, based on climatic dissimilarity indices and provenance–site matching. Their method provides a clear foundation for anticipating the adaptive potential of seed sources. This approach complements ForesteCCo, which extends this perspective by explicitly modelling the climatic suitability of provenance-based genetic groups to explore potential intra-specific differences in climatic responses across space and time. Together, both perspectives highlight the importance of integrating genetic provenance information into restoration strategies, recognising that provenance-based selection and genetic-group modelling constitute complementary pathways to support resilience-oriented and climate-smart forest management under future climate conditions.

Similar principles have been demonstrated in experimental forest management contexts. Holbrook and Puhlick (2025) tested assisted migration strategies in *Pinus palustris* and *Quercus laevis*, showing that selecting seed material from warmer provenances can enhance survival and regeneration following disturbance events. Their results provide practical evidence that adaptive provenance transfer can maintain species composition and ecological identity while improving resilience to future conditions.

Within this perspective, ForesteCCo contributes by quantifying variations in the climatic suitability of genetic groups along environmental gradients, thereby revealing potential mismatches between projected conditions and existing local populations

D *Quercus ilex* –Analusia GG1

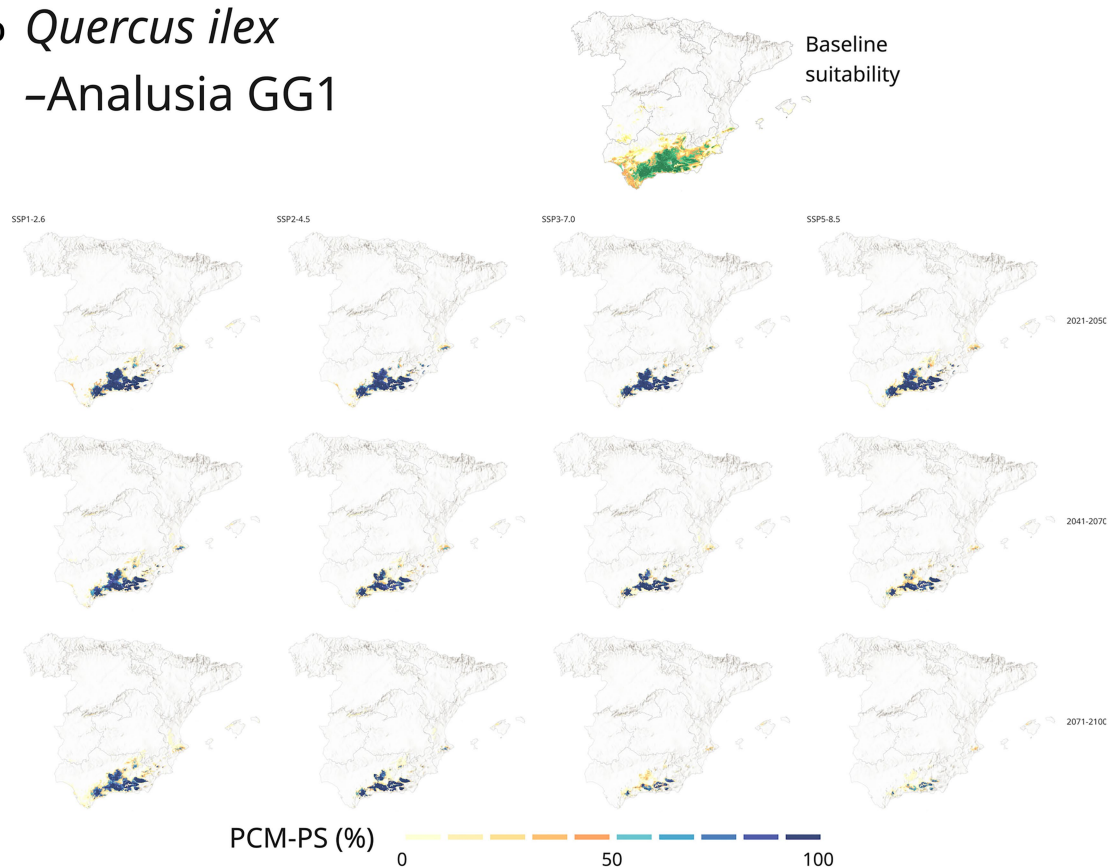


FIGURE 6

Synthesised projections of climatic suitability using the percentage of climate models predicting suitability (PCM–PS) for two species: (A) *Arbutus unedo*, (B) *Quercus canariensis*, and two genetic groups: (C) *Pinus sylvestris* Eastern GG3, (D) *Quercus ilex* Andalusia GG1). Maps show baseline conditions (1985–2014) and future projections across three time horizons under four SSPs of the percentage of climate models predicting suitability (PCM–PS).

(Aitken et al., 2008). It is relatively common for projections to indicate areas where the future climate may become unsuitable for the resident genetic group, yet remain suitable for another group of the same species (Breed et al., 2013). Such insights enable managers to consider alternative provenances that are climatically compatible and resilient, without altering the species identity or the cultural and ecological attributes of the landscape. However, this also presents a significant policy challenge, since forestry regulations often mandate the exclusive use of local seed sources—an approach that may inadvertently constrain adaptive potential if future climate projections indicate low persistence for those local lineages (Broadhurst et al., 2008).

An illustrative example can be seen in the spatial distribution of the different genetic groups of *Pinus halepensis* (Figure 7). When one of these groups—specifically, genetic group 3 from southern Spain (gg3, Figure 7a)—is modelled independently (Figure 7b), the resulting pattern more accurately reflects the actual distribution of individuals belonging to that lineage than the model calibrated with all species occurrences (Figure 7c). In the species-level model, several occurrences of gg3 are not properly represented (red points in Figure 7c), whereas the genetic-group model successfully captures these presences (black points in Figure 7b). Moreover, the model for gg3 identifies additional areas of potential suitability that remain undetected when modelling the species as a whole.

This improvement stems from the fact that models calibrated for a specific genetic group more accurately capture the local climatic conditions under which those populations have adapted. In contrast, when the SDM is trained using all presence data without genetic differentiation, highly distinct climatic conditions become “blended,” reducing both predictive accuracy and reliability—particularly for populations adapted to more extreme environments, as evidenced by the higher proportion of unpredicted presences (red points) along the distribution borders.

Comparable patterns of adaptive differentiation have been documented in forest ecosystems worldwide. For example, Zhu et al. (2025) identified distinct climatic refugia for multiple Fagaceae species in China, showing how intra-lineage variability can contribute to persistence under warming scenarios. The ForesteCCo results are consistent with this perspective, indicating that taxa with broader ecological amplitudes tend to exhibit greater spatial stability under future climates than narrowly distributed or cold-adapted species. By explicitly modelling genetic groups, the framework links climatic suitability projections with provenance-based differentiation, moving beyond species-level analyses and enabling a more refined interpretation of resilience. Rather than assuming direct measures of adaptive fitness, this approach provides a spatially explicit representation of where different genetic configurations may remain climatically compatible under future conditions.

TABLE 4 Overview of species-specific dominant trends and spatial responses to future climate scenarios.

Species scientific name	Distribution	Dominant trend	Trend type	CC responses	Spatial trend
<i>Abies pinsapo</i>	Restricted distribution	Contraction (25)	Accelerated decline (10)	Severely contracting (10)	IS disappearance (1)
<i>Betula pubescens</i>	Atlantic				LC(5)
<i>Juniperus thurifera</i>	Montane & subalpine				
<i>P. uncinata</i>	Montane & subalpine				
<i>Sorbus aria</i>	Montane & subalpine				
<i>Sorbus aucuparia</i>	Montane & subalpine				
<i>Acer pseudoplatanus</i>	Montane & subalpine				US(4)
<i>Fraxinus angustifolia</i>	Widespread				
<i>Ilex aquifolium</i>	Montane & subalpine				
<i>Juniperus communis</i>	Montane & subalpine				
<i>Fraxinus excelsior</i>	Montane & subalpine		Monotonic decline (10)	Mod. resilient (1)	IS-p
<i>Juglans regia</i>	Widespread			Vulnerable (9)	LC(7)
<i>Juniperus oxycedrus</i>	Mediterranean				
<i>Prunus avium</i>	Montane & subalpine				
<i>Q. coccifera</i>	Mediterranean				
<i>Taxus baccata</i>	Montane & subalpine				
<i>Tilia platyphyllos</i>	Montane & subalpine				US(2)
<i>Ulmus glabra</i>	Montane & subalpine				
<i>Castanea sativa</i>	Mediterranean				
<i>Populus tremula</i>	Montane & subalpine				
<i>Acer platanoides</i>	Montane & subalpine				
<i>Tilia cordata</i>	Montane & subalpine		Non-monotonic or Non-monotonic with transient recovery (5)	Severely contracting (2)	LC(2)
<i>Abies alba</i>	Montane & subalpine			Vulnerable (1)	Upward shift
<i>Ulmus minor</i>	Widespread			Moderately resilient (2)	LE
<i>Betula pendula</i>	Montane & subalpine				Upward shift
<i>Alnus glutinosa</i>	Widespread	Persistence (1)	Non-monotonic with transient recovery	Highly resilient	IS-p
<i>Arbutus unedo</i>	Widespread	Expansion (6)	Monotonic increase (1)	Highly resilient (1)	LE
<i>Q. pubescens</i>	Montane & subalpine		Non-monotonic with stabilisation (1)	Expanding (potential coloniser) (5)	Upward shift
<i>Populus nigra</i>	Montane & subalpine		Strong expansion (exponential-like) (4)		LE
<i>Populus alba</i>	Widespread				LE (2)
<i>Q. canariensis</i>	Restricted distribution				WE
<i>Tamarix gallica</i>	Mediterranean				

Species are classified according to their dominant trend (contraction, persistence, or expansion), temporal trend type (e.g., monotonic decline, non-monotonic recovery), climate-change response category, and observed spatial trend (e.g., upward shift, lowland contraction, latitudinal or westward expansion).

TABLE 5 Overview of dominant trends and spatial responses of genetic groups (GGs) under projected climate scenarios.

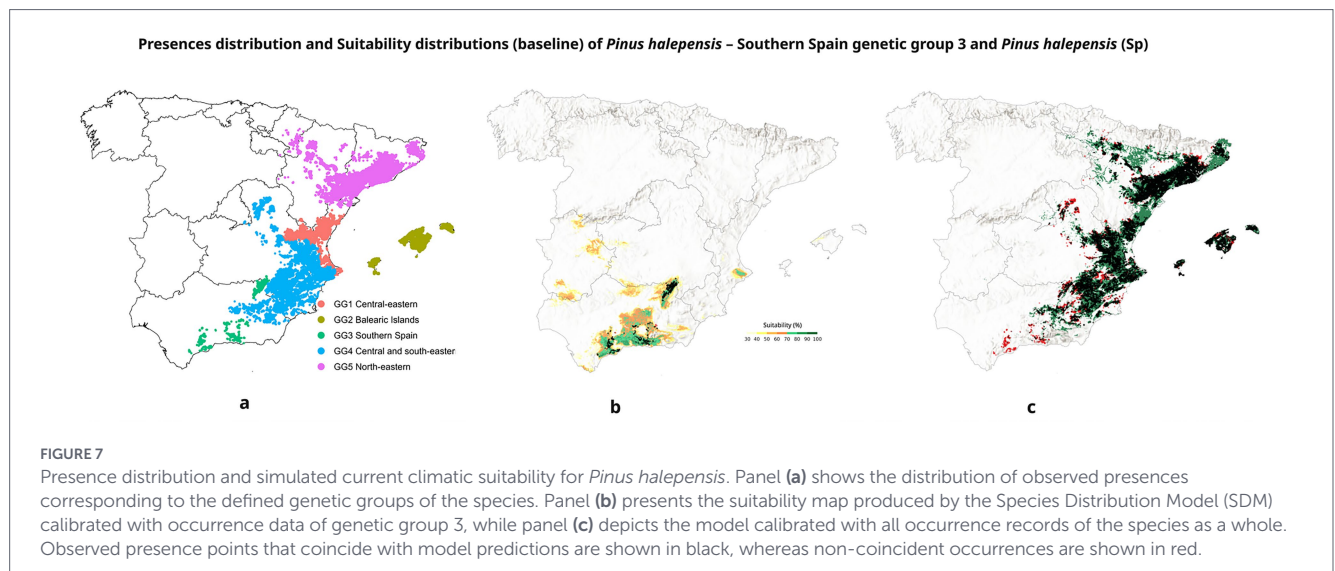
Genetic group name	GG Provenance regions	Dominant trend	Trend type	Climate-change response	Spatial trend
<i>F. sylvatica</i> GG1	Galicia	Contraction (36)	Accelerated decline (25)	Severely contracting (25)	LC(23)
<i>F. sylvatica</i> GG3	Central Spain				
<i>P. halepensis</i> GG3	Southern Spain				
<i>P. halepensis</i> GG4	Central and Northern Spain				
<i>P. sylvestris</i> GG1	Western				
<i>P. sylvestris</i> GG3	Eastern				
<i>Q. faginea</i> GG2	Temperate Mediterranean				
<i>Q. faginea</i> GG3	Cool Continental				
<i>Q. ilex</i> GG1	Andalusia				
<i>Q. ilex</i> GG2	Eastern Sierra Morena–Alicante				
<i>Q. ilex</i> GG3	Central Sierra and Both Plateaus				
<i>Q. ilex</i> GG5	Teruel				
<i>Q. ilex</i> GG7	Cantabrian–La Rioja				
<i>Q. petraea</i> GG1	Western				
<i>Q. petraea</i> GG2	Basque–Navarre/Interior Sierras				
<i>Q. pyrenaica</i> GG1	Atlantic				
<i>Q. pyrenaica</i> GG2	Sub-Mediterranean Continental				
<i>Q. pyrenaica</i> GG3	Temperate–Humid Sub-Mediterranean				
<i>Q. robur</i> GG1	Cantabrian				
<i>Q. robur</i> GG2	Western Pyrenean/Iberian				
<i>Q. robur</i> GG3	Eastern Pyrenean				
<i>Q. suber</i> GG2	Western Core				
<i>Q. suber</i> GG3	Southwestern Core				
<i>P. pinea</i> GG1	Northern Plateau				US(2)
<i>P. pinea</i> GG2	Eastern				
<i>F. sylvatica</i> GG2	Pyrenees		Monotonic decline (3)	Vulnerable (2)	LC(2)
<i>P. pinaster</i> GG2	Central Spain			Moderately resilient (1)	IS-p
<i>Q. suber</i> GG4	Southern Spain				

(Continued)

TABLE 5 (Continued)

Genetic group name	GG Provenance regions	Dominant trend	Trend type	Climate-change response	Spatial trend
<i>P. halepensis</i> GG2	Balearic Islands		Non-monotonic with transient recovery (8)	Severely contracting (2)	LC(2)
<i>Q. ilex</i> GG8	Balearic Islands			Vulnerable (4)	LE (2)
<i>P. halepensis</i> GG1	Central and Southern Spain				
<i>P. pinaster</i> GG4	Southern Spain				
<i>P. nigra</i> GG2	Central			Moderately resilient (2)	LC(2)
<i>Q. pyrenaica</i> GG4	Warm Continental				LC(2)
<i>P. nigra</i> GG3	Southeastern				
<i>P. pinaster</i> GG1	Atlantic Iberian				
<i>P. pinaster</i> GG3	Eastern Spain	Persistence (4)	Non-monotonic or Non-monotonic with transient recovery (4)	Highly resilient (4)	Upward shift
<i>P. sylvestris</i> GG2	Pyrenean				IS-p
<i>Q. faginea</i> GG1	Cantabrian–Pyrenean				LC
<i>Q. suber</i> GG1	Northwestern				WE
<i>P. halepensis</i> GG5	Northern Spain and France	Expansion (9)	Non-monotonic or Non-monotonic with stabilisation (5)	Highly resilient (2)	IS-p
<i>Q. petraea</i> GG3	Eastern Pyrenean				Upward shift
<i>P. pinea</i> GG4	Catalonia			Expanding (potential coloniser) (3)	LE
<i>P. pinea</i> GG3	Andalusia				US(2)
<i>Q. ilex</i> GG6	Catalonia–Valencia		Strong expansion (exponential-like) (4)	Expanding (potential coloniser) (4)	IS-p
<i>Q. faginea</i> GG4	Sub-humid Continental				LE
<i>Q. ilex</i> GG4	Western				US(2)
<i>P. nigra</i> GG1	Northeastern				
<i>Q. suber</i> GG5	Eastern				

Each GG is classified according to its dominant trend (contraction, persistence, or expansion), temporal trend type (e.g., accelerated decline, non-monotonic recovery), climate-change response category, and predominant spatial trend (e.g., lowland contraction, upward shift, latitudinal expansion, westward expansion).



Spatial patterns and climate-driven suitability shifts

The spatial patterns derived from the ForesteCCo models reveal a coherent reorganisation of climatic suitability across the Iberian Peninsula. Most taxa show contractions in areas currently characterised by cool and humid climates, coupled with gains or relative stability in Mediterranean and lower-latitude zones. Approximately 78% of species and 73% of genetic groups are projected to lose suitable area under future conditions, while only a minority—primarily thermophilous taxa—exhibit persistence or moderate expansion. This contrast reflects a consistent climatic filtering effect, whereby warming and increasing aridity favour drought-tolerant species over taxa restricted to cooler and mesic environments.

These projections align with previous Iberian-scale assessments. National modelling studies predicted marked reductions for mountain conifers such as *Pinus sylvestris*, *P. uncinata*, and *Abies alba*, as well as for temperate broadleaves including *Fagus sylvatica* (Benito Garzón et al., 2008). High-resolution analyses in Mediterranean mountains projected upward migration of Mediterranean taxa and severe losses of climatically suitable areas for cold-adapted species (Ruiz-Labourdette et al., 2011). Similarly, del Río et al. (2018) highlighted the vulnerability of Spanish *Fagus sylvatica* forests to warming and declining precipitation. The spatial signals identified by ForesteCCo are therefore consistent with accumulated empirical evidence.

At regional scale, northern and high-elevation areas—particularly the Cantabrian Mountains, Pyrenees, and Central System—emerge as zones of relative persistence. These mountain systems act as climatic retention areas, buffering regional warming. In contrast, Mediterranean species such as *Quercus ilex*, *Q. canariensis*, and *Pinus halepensis* display more stable or moderately expanding suitability patterns, suggesting greater tolerance to warmer and drier regimes.

ForesteCCo also identifies potential climate-resilient refugia where suitability remains high and model agreement (PMC–PS) is strong. These areas are concentrated in mountainous and transitional coastal zones, consistent with the role of topographic heterogeneity in generating microclimatic buffering (Ruiz-Labourdette et al., 2011). Comparable refugial dynamics have been documented elsewhere; for

example, Zhu et al. (2025) identified climatically stable areas for *Fagaceae* species in China under future warming scenarios.

Across scenarios, most taxa retain roughly 30–35% of their current suitable area, with gains (20–25%) concentrated in northern and higher-elevation regions and losses predominating in lowland and continental sectors. The explicit modelling of genetic groups refines these spatial patterns by revealing intra-specific differentiation in climatic trajectories, adding resolution to the broader biogeographical signal documented for Iberian forests.

When considered as a whole, the spatial configuration of projected changes reveals a scale-consistent signal of climate-driven biogeographical reorganisation across Iberia. The alignment between continental projections and ForesteCCo's regional results emphasises both the universality of climate-filtering mechanisms and the key influence of genetic diversity in shaping local responses. These insights provide a robust spatial basis for designing climate-resilient forest networks and adaptive restoration strategies.

Implications for restoration and adaptive planning

The ForesteCCo framework provides a comprehensive and operational tool to support restoration and adaptive management of forest ecosystems under climate change. By modelling not only species but also their genetic groups, the framework provides a dual perspective that bridges ecological realism with practical decision-making, capturing both interspecific and intra-specific dimensions of climate adaptation. The species included in the analysis correspond to those identified by national and regional administrations as key components of Spain's green infrastructure, ensuring the relevance of the results for policy and management. Beyond species-level patterns, the inclusion of genetic groups adds an essential adaptive layer, representing forest lineages already established and adapted to their regional climates. These lineages constitute valuable sources for seed collection and provenance-based reforestation, helping to maintain local ecological integrity while enhancing resilience to future conditions.

Operating at high spatial resolution and integrating multiple global climate models, socioeconomic pathways, and temporal horizons, the ForesteCCo system captures both the magnitude and the

uncertainty of projected changes across Spain. This multi-scenario approach allows users to explore alternative futures, assess model confidence, and align decisions with their risk tolerance or planning horizon. As such, the web platform developed to deliver all the results provides flexibility for diverse actors—public administrations, forest enterprises, conservation agencies, and local communities—to tailor their interventions based on robust scientific results.

From a practical standpoint, the outputs of ForesteCCo can be used in multiple ways. Managers can identify areas where the continuity of forest cover is crucial for maintaining ecosystem services, and anticipate which species—or genetic groups—are likely to remain viable under near-future climates. Conversely, the framework highlights areas at risk of suitability loss, allowing for proactive adaptation strategies such as assisted migration, enrichment planting, or diversification of species assemblages. Holbrook and Puhlick (2025) demonstrated that using climatically pre-adapted provenances can enhance post-disturbance survival while preserving forest structure and function. Likewise, Ameztegui et al. (2024) provided a quantitative basis for provenance selection in Mediterranean species, a concept now expanded at the national scale by ForesteCCo.

The multi-temporal projections also support adaptive cycles of monitoring and planning. By offering time-slice comparisons (2021–2050, 2041–2070, 2071–2,100), users can evaluate short-, mid-, and long-term risks, aligning management interventions with the pace of projected changes. This is particularly relevant for long-lived species, where planning decisions made today will determine forest composition for decades to come. Such integration of forward-looking evidence supports the transition from reactive to anticipatory management.

Importantly, the framework also serves as a bridge between scientific modelling and applied restoration. By translating ensemble modelling outputs into accessible maps and synthetic indicators—such as suitability stability, gain–loss patterns, and model agreement (PMC–PS)—ForesteCCo converts complex climatic and ecological projections into decision-ready information. Rather than remaining at the level of abstract suitability estimates, the framework operationalises uncertainty and spatial dynamics in ways that are directly interpretable for management. Through this synthesis, restoration practitioners can move beyond static notions of “potential vegetation” and towards dynamic, climate-smart planning grounded in robust, scenario-based, and uncertainty-aware projections.

Ultimately, the ForesteCCo approach enables adaptive forest restoration at multiple scales: identifying species and genetic materials suitable for each region, maintaining the continuity of the national green infrastructure, and fostering resilient landscapes capable of sustaining ecological and socio-economic functions under a changing climate.

Limitations and future directions

While the ForesteCCo framework represents a significant methodological advance in integrating species and genetic-level modelling for adaptive forest planning, several limitations and future challenges remain. The 1 × 1 km spatial resolution, although appropriate for national-scale analyses, does not capture the fine-scale environmental heterogeneity that can strongly influence local suitability. Topographic complexity, hydrological gradients, and microclimatic conditions along river corridors or shaded slopes are crucial factors that may

substantially refine habitat projections. This limitation is particularly evident for narrowly distributed endemics such as *Abies pinsapo*, which, according to our results, may lose all suitable habitat by the end of the century. A finer-scale study could likely identify microrefugia and key sites for its persistence and conservation, illustrating the importance of scaling down to capture local resilience processes.

Another source of uncertainty arises from the occurrence data themselves. Approximately 5–10% of presence records were not included in model calibration, reflecting the inevitable spatial and taxonomic biases present in large biodiversity datasets. This highlights that, regardless of their statistical robustness, species distribution models always carry a degree of interpretative error that must be acknowledged when transferring results into management decisions.

Moreover, species distributions cannot be fully explained by environmental variables alone. Physiological traits, behavioural responses, and ecological processes such as competition, facilitation, and symbiosis all contribute to shaping realised niches (Guisan and Zimmermann, 2000). These dimensions are still largely absent from most correlative modelling frameworks, including ours, primarily due to data limitations and the difficulty of quantifying such interactions at broad scales. As Elith and Leathwick (2009) emphasised, bridging data- and process-based approaches remains an essential step towards a more mechanistic understanding of biodiversity–climate relationships. Integrating eco-physiological and demographic drivers into future iterations of ForesteCCo will therefore be a major research frontier. In addition, several key external drivers that strongly condition forest dynamics were not explicitly considered in the present implementation of the framework. Land-use change, anthropogenic pressure, and disturbance regimes such as wildfire can substantially alter habitat availability and connectivity, independently of climatic suitability. In this regard, climate is recognised as the primary hierarchical filter determining species' potential distribution at regional to national scales, while local persistence is further modulated by finer-scale drivers such as disturbance regimes. Likewise, climate-related extreme events, including floods and droughts, may impose abrupt constraints on forest persistence that are not captured by long-term mean climate projections. These factors can interact with climate change in non-linear ways and may further limit or redirect restoration outcomes at local and regional scales. Incorporating such drivers through scenario-based approaches or coupled modelling frameworks represents an important avenue for future development and would further enhance the applicability of ForesteCCo to real-world forest planning and restoration.

Another important limitation that is already being addressed in ongoing work relates to riparian species and communities, which depend not only on the climatic and soil factors that have been included in this study, but also, and perhaps more importantly, on ecohydrological factors such as water tables, flow rates, periods of flooding and drought, etc. Ultimately, these limitations do not diminish the value of the current approach but rather outline a roadmap for its evolution. ForesteCCo establishes a strong foundation upon which finer-scale, process-based, and community-level analyses can be built—advancing towards a new generation of spatially explicit, climate-informed tools for forest conservation and adaptive management.

Future work should address critical challenges, among which scaling across spatial and temporal dimensions will be essential. As mentioned, increasing spatial resolution—potentially to 200 meters—would allow the incorporation of fine-grain environmental variables and enhance the detection of microclimatic refugia. The

platform's outputs could then be expanded to support more detailed assessments of climate-resilient biodiversity refugia and to inform the redesign of ecological corridors that ensure continuity between present and future suitable areas. Additionally, moving beyond single-species projections towards analyses of future forest community composition will be crucial to understand how assemblages may reorganise under changing climates. Incorporating eco-physiological data and functional traits into these models will further improve their predictive realism and relevance for adaptive restoration.

Conclusion

The ForesteCCo initiative provides a robust, integrative modelling framework for assessing how climate change may reshape the distribution and adaptive capacity of Iberian Forest species. By combining ensemble modelling across climate models, scenarios, and temporal horizons with a genetics-informed stratification of taxa, it offers a rare integration of climatic, ecological, and evolutionary information at the national scale. The focus on genetic groups enhances both predictive accuracy and practical relevance for provenance-based restoration and adaptive forest management. Improvements in the input variables of SDMs, as well as the use of a consensus strategy in such modelling, have made it possible to improve the reliability of their results.

The results reveal a consistent biogeographical reorganisation driven by climatic warming, with more than 70% of the analysed forest species and genetic groups exhibiting contraction trends under future scenarios. These contractions are particularly pronounced among temperate and montane taxa, whereas Mediterranean and drought-tolerant species tend to show greater persistence or, in some cases, expansion. The identification of climatically resilient refugia, especially in northern and high-elevation regions, provides a spatial foundation for prioritising conservation and restoration efforts. The framework's incorporation of model agreement metrics (PCM–PS) further strengthens confidence in identifying areas of high climatic stability and potential connectivity under future conditions.

Beyond its immediate results, ForesteCCo contributes conceptually to the emerging paradigm of climate-smart restoration. By translating complex ensemble outputs into decision-ready products, it bridges science and practice, helping planners select suitable species, genetic materials, and sites to maintain the functionality of Spain's green infrastructure under changing climates. All resulting data, maps, and indicators are accessible through a public web-based viewer, ensuring transparency, reproducibility, and broad usability for forest managers, researchers, and decision-makers. The next steps—refining models with eco-physiological and community-level data, increasing spatial resolution, integrating ecohydrological variables for riparian species, and enhancing the integration of local monitoring—will extend the platform's utility and support a new generation of climate-informed forest planning across southern Europe.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/[Supplementary material](#).

Author contributions

EC-M: Conceptualization, Methodology, Software, Investigation, Writing – review & editing, Formal analysis, Writing – original draft, Visualization. RA: Writing – review & editing, Data curation. MF-P: Software, Writing – review & editing, Visualization. EG: Formal analysis, Writing – review & editing, Software. JG: Methodology, Data curation, Writing – review & editing, Conceptualization, Funding acquisition. RM: Funding acquisition, Formal analysis, Writing – review & editing, Investigation, Software, Conceptualization, Methodology. AG: Writing – review & editing, Software. DG: Writing – review & editing, Data curation. CG-P: Data curation, Writing – review & editing, Formal analysis, Software. AH-P: Writing – review & editing, Resources. JM-B: Formal analysis, Methodology, Data curation, Software, Writing – review & editing. CPA: Writing – review & editing, Software, Formal analysis. CP-r: Formal analysis, Software, Writing – review & editing, Data curation. JR-B: Writing – review & editing, Funding acquisition, Methodology. JR: Visualization, Conceptualization, Project administration, Methodology, Writing – review & editing, Funding acquisition, Supervision. GR-R: Software, Visualization, Methodology, Writing – review & editing, Formal analysis. DR: Visualization, Software, Writing – review & editing. SO: Data curation, Writing – review & editing. MC: Writing – review & editing, Funding acquisition, Project administration, Conceptualization, Supervision, Investigation.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2026.1735354/full#supplementary-material>

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