

Article

Assessing Potential Changes in the Distribution of Major Warm–Temperate Tree Species in South Korea Under Climate Change Scenarios

Jong-Hoon Park ¹ , Jeong-Gwan Lee ¹ , Han Doo Shin ² , Hee-Jin Lee ¹, Du-Hee Lee ³ , Su Hyeon Eum ¹ and Hyun-Jun Kim ^{1,*} 

- ¹ Department of Forest Resources, Chonnam National University, Gwangju 61187, Republic of Korea; jonghoonpark0105@gmail.com (J.-H.P.); gwaanee@gmail.com (J.-G.L.); heejin.lee322@gmail.com (H.-J.L.); eumwoods@gmail.com (S.H.E.)
 - ² Department of Agriculture, Forestry and Bioresources, Seoul National University, Seoul 08826, Republic of Korea; rhduddk84@snu.ac.kr
 - ³ Korea Environment Institute, Bldg B, 370 Sicheong-daero, Sejong 30147, Republic of Korea; dhuee2@gmail.com
- * Correspondence: hjkim0837@jnu.ac.kr; Tel.: +82-62-530-2082

Abstract

Climate change drives shifts in forest vegetation zones, and the major tree species of warm–temperate evergreen broad-leaved forests in South Korea are also expected to undergo changes in their potential distributions under future climate conditions. This study applied a Committee Averaging (CA) ensemble species distribution model to *Quercus acuta*, *Machilus thunbergii*, *Quercus glauca*, and *Castanopsis sieboldii* to project changes in their potential distributions under four Shared Socioeconomic Pathway (SSP) scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) across two future periods (2050s and 2090s). To compare interspecific differences in response more clearly, we applied a two-tier threshold scheme that distinguished potential habitat (agreement ≥ 0.6) from highly suitable habitat (> 0.8), and we concurrently conducted a Multivariate Environmental Similarity Surface (MESS) analysis to assess predictive uncertainty arising from extrapolation into future climates. The CA ensemble models showed excellent predictive performance (AUC 0.947–0.989; TSS 0.837–0.943). For *Q. acuta*, *M. thunbergii*, and *Q. glauca*, potential habitat expanded consistently across all SSP scenarios, and highly suitable habitat shifted northward into parts of the central and Gangwon regions. In contrast, both the potential habitat and the highly suitable habitat of *C. sieboldii* contracted under most future scenarios. These results demonstrate that even species belonging to the same warm–temperate evergreen broad-leaved forest community can respond differently to future climate. The two-tier threshold scheme applied in this study was effective not only for assessing whether distributions expand but also for delineating and evaluating climatically stable core habitats. Although our findings need to be interpreted in light of the uncertainty associated with extrapolation into future climates, they can serve as useful baseline data for establishing climate-change-adaptive forest conservation and species-specific management strategies.

Keywords: species distribution model; ensemble; committee averaging; range shift; core habitat; individualistic response; extrapolation uncertainty



Academic Editor: Hubert Hasenauer

Received: 13 July 2026

Revised: 7 August 2026

Accepted: 19 August 2026

Published: 21 August 2026

Copyright: © 2026 by the authors.

Licensee MDPI, Basel, Switzerland.

This article is an open access article

distributed under the terms and

conditions of the [Creative Commons](https://creativecommons.org/licenses/by/4.0/)

[Attribution \(CC BY\)](https://creativecommons.org/licenses/by/4.0/) license.

1. Introduction

Climate change is a major environmental driver altering the structure and function of ecosystems, and forest ecosystems are responding sensitively to it [1]. In particular, rising temperatures, shifting precipitation patterns, and an increasing frequency of extreme weather events affect the distributional ranges and habitat suitability of tree species, driving shifts in forest vegetation zones [2,3]; these shifts can lead to a reorganization of forest ecosystems accompanied by increased tree mortality and changes in vegetation structure [4]. South Korea lies within the East Asian monsoon climate zone and exhibits pronounced climatic gradients across a relatively small land area, arising from latitude, maritime and continental air masses, and mountainous topography [5]. These environmental characteristics form a compressed distribution of diverse vegetation zones ranging from boreal vegetation to warm-temperate evergreen broad-leaved forests [6], providing conditions under which climate-driven shifts in vegetation zones may become apparent within a relatively short period. Therefore, to manage forest resources and maintain ecosystem function in South Korea, studies projecting species-specific changes in potential distribution under future climate conditions are needed [7].

Warm-temperate evergreen broad-leaved trees are a group of species adapted to warm climate conditions, and in South Korea they are distributed mainly along the southern coast and on offshore islands. They constitute the forest ecosystems of the southern region and perform diverse ecosystem functions, including carbon uptake and storage and the maintenance of biodiversity [8]. Because their northern distributional limits are governed primarily by winter low-temperature thresholds [9–11], an expansion of their potential distribution is expected as temperatures rise. The four target species of this study—*Quercus acuta*, *Machilus thunbergii*, *Quercus glauca*, and *Castanopsis sieboldii*—are major dominant species that account for about 63% (6110 ha) of the country's warm-temperate evergreen broad-leaved forests (approximately 9700 ha) [12]. They are known as key species in the successional sequence of Korean warm-temperate forests—with *M. thunbergii* forming the intermediate stage and *Q. acuta* and *C. sieboldii* forming the climax stage—and thus occupy an important position in determining the species composition and structure of warm-temperate evergreen broad-leaved forests [8]. Meanwhile, having undergone prolonged anthropogenic disturbance such as past fuelwood harvesting, most of South Korea's warm-temperate evergreen broad-leaved forests have been converted into secondary forests or substitute vegetation dominated by *Pinus thunbergii* and deciduous oaks, leaving only a limited number of stands maintained in a natural state [8]. Accordingly, the use of native species in the restoration of degraded lands and the establishment of forest resources has been emphasized, and these four species have likewise been selected as key regeneration species for developing forest resources in response to climate change [12]. Moreover, because natural forests account for approximately 95% of extant warm-temperate evergreen broad-leaved forests and thus most stands have been maintained naturally [12], potential distribution projections using occurrence data for these four species can relatively well reflect the species' native site conditions.

Species distribution models (SDMs) have been widely used as a representative tool for projecting species-specific changes in potential distribution. An SDM estimates current and future potential distributions based on the statistical relationship between species occurrence data and environmental variables, and a wide range of models—from statistical to machine learning-based approaches—are employed [13,14]. However, because individual models are based on differing statistical assumptions and learning structures, their predictions can diverge even for the same data [7,15]; in particular, under future climate conditions that fall outside the environmental range of the training data, the discrepancies among models increase, making it difficult to reliably interpret changes in potential distri-

bution from a single model alone [16]. To address this limitation, ensemble approaches that integrate the results of multiple individual models have been proposed [17]; by relaxing the dependence on individual model assumptions and reducing predictive variability, ensembles enable more stable predictions [18]. Ensemble methods include simple averaging of suitability values, weighted averaging that reflects model performance, and committee averaging (CA), which computes the level of agreement among binarized presence–absence predictions [19–21]. Among these, CA intuitively expresses the degree to which multiple models jointly predict presence as a per-pixel agreement value (0–1), making it advantageous for spatially delineating and assessing the level of predictive reliability [22]. This characteristic goes beyond simply determining whether a distribution expands, providing a basis for interpreting the interior of a potential distribution in finer detail according to the level of agreement.

In South Korea, studies projecting future distributions of warm–temperate tree species using SDMs have been carried out steadily [23–27]. However, many of these studies focused on species presence or the outward expansion of the distributional range, and qualitative changes within the distribution were not sufficiently addressed. Within a potential distribution lies a core area, characterized by high inter-model agreement, where a species can establish stably; even when the distributional range expands geographically, the area of this core region may instead decrease or shift spatially, and such patterns may differ among species even within the same warm–temperate species group [24]. Therefore, an approach is needed that assesses changes in total distributional area and changes in the core region separately yet jointly, and that quantitatively compares interspecific differences in response within a single analytical framework. In addition, previous domestic studies have rarely explicitly assessed and reported the risk of extrapolation arising when future climates fall outside the training range of the model, and thus approaches that present prediction results together with extrapolation risk have also been lacking. For future distribution projections to serve as a basis for forest management decision-making, it is necessary to present, alongside the direction of the prediction, whether that prediction is grounded in the environmental range of the training data or instead constitutes extrapolation [28].

Accordingly, this study aims to combine the CA ensemble technique with an agreement-based two-tier threshold scheme to project climate-change-driven changes in the potential distributions of major warm–temperate tree species in South Korea and to jointly assess the uncertainty of those projections. Specifically, for *Quercus acuta*, *Machilus thunbergii*, *Quercus glauca*, and *Castanopsis sieboldii*, we (1) quantify changes in the area and spatial distribution of potential habitat (agreement ≥ 0.6) and highly suitable habitat (> 0.8) across the SSP scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) and future periods (2050s and 2090s), (2) compare interspecific differences in response within a single analytical framework, and (3) assess predictive uncertainty arising from extrapolation into future climates through Multivariate Environmental Similarity Surface (MESS) analysis. By addressing these objectives, this study provides baseline data for establishing forest conservation and management strategies that reflect interspecific differences in response and predictive uncertainty even within the same species group, in preparation for climate-change-driven shifts in forest vegetation zones.

2. Materials and Methods

2.1. Study Area and Target Species

South Korea is located at 33–39° N and 124–132° E, with a mean annual temperature of 12.8 °C and an annual precipitation of 1306 mm based on the climatological normals (1991–2020) [29]. The study area was restricted to forest land, which corresponds to approximately 63% of the country's territory [30], and this spatial extent was extracted based on the

1:5000 Forest Type Map distributed by the Korea Forest Service [31]. *Quercus acuta*, *Machilus thunbergii*, *Quercus glauca*, and *Castanopsis sieboldii* were selected for analysis (Figure 1). Occurrence points for each species were extracted based on data from the 7th National Forest Inventory (NFI, 2016–2020). The NFI is a survey that places fixed sample plots across forests nationwide following a systematic sampling design at $4\text{ km} \times 4\text{ km}$ intervals, giving the sample plots a spatially even distribution. To supplement the sample size of warm-temperate species, which is concentrated in the southern region, vascular plant distribution data from the 5th National Ecosystem Survey (NES, 2019–2023) were additionally merged. To match the 1 km^2 ($0.01^\circ \times 0.01^\circ$) spatial resolution of the climate data, grid-based spatial thinning was applied to the collected occurrence points, consolidating multiple occurrence points within the same grid cell into one. The final occurrence points used in the analysis numbered 30 for *Q. acuta*, 106 for *M. thunbergii*, 35 for *Q. glauca*, and 41 for *C. sieboldii*.

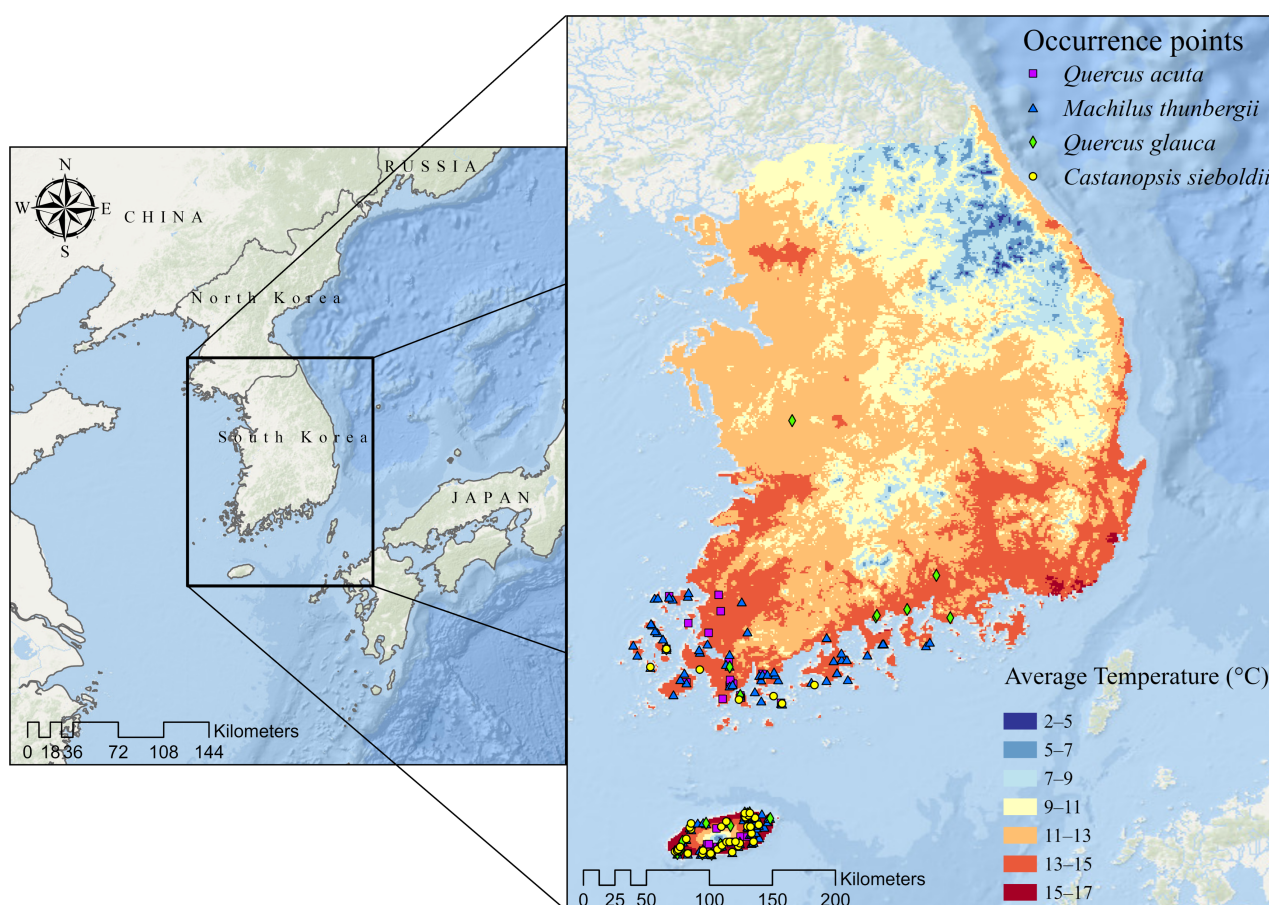


Figure 1. Study area with mean annual temperature and species occurrence points.

2.2. Environmental Variables and Variable Selection

To project changes in the potential distributions of the species using species distribution models, we derived climate, topographic, and soil variables capable of reflecting the physiological limits and ecological requirements of the target species and included them as model inputs. For climate variables, we used present (2000–2019) climate data based on the Korea Meteorological Administration’s MK-PRISM v2.1 and SSP-scenario-based future data (2050s: 2041–2060; 2090s: 2081–2100). The applied SSP scenarios are classified into four types according to greenhouse gas emission intensity and socioeconomic development pathways: SSP1-2.6 (low emissions, sustainability), SSP2-4.5 (intermediate emissions, middle-of-the-road), SSP3-7.0 (high emissions, regional rivalry), and SSP5-8.5

(very high emissions, fossil-fuel-driven) [32,33]. From the present and future climate data, we derived 19 bioclimatic variables (BIO1–BIO19) (Table 1). Among these, BIO1 and BIO6 were included in common for all species, given that they are key variables representing, respectively, the overall thermal environment and the winter low-temperature limit of warm-temperate species. For the remaining bioclimatic variables, species-specific correlation analyses were performed to prevent multicollinearity and reduce uncertainty due to extrapolation [34], and only variables with an absolute correlation coefficient ($|r|$) below 0.7 with BIO1 and BIO6 were additionally included in the models. For the finally selected variables, variance inflation factors (VIFs) were computed and verified to all be below 5 [34].

Table 1. Description of bioclimatic variables (BIO1–BIO19).

Variable	Description
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (mean of monthly (max temp – min temp))
BIO3	Isothermality (BIO2/BIO7) ($\times 100$)
BIO4	Temperature Seasonality (standard deviation $\times 100$)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5 – BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (coefficient of variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Topographic variables were included to complement site-specific characteristics that are difficult to explain with climate variables alone [35]. Using the 90 m Digital Elevation Model (DEM) provided by the National Geographic Information Institute (www.ngii.go.kr), we computed altitude, the Topographic Position Index (TPI), and the Topographic Wetness Index (TWI) in ArcGIS Pro (ver. 3.5.0; Esri, Redlands, CA, USA). TPI was calculated as the difference between the elevation of the central cell and the mean elevation of its 3×3 neighborhood [36]. TWI was derived by filling depressions in the DEM, computing flow direction and flow accumulation with the D8 algorithm to obtain the upslope contributing area, and combining this with the local slope [37].

Soil variables were obtained from the ISRIC database (data.isric.org) at a 250 m spatial resolution. To represent the topsoil conditions that directly influence early establishment and growth of the target species, soil pH and clay content were extracted and included as predictors [38]. The topographic and soil variables were resampled to a 1 km^2 spatial resolution ($0.01^\circ \times 0.01^\circ$) using bilinear interpolation to ensure spatial consistency with the climate variables and to match the input resolution of the species distribution models. All layers were unified under the WGS 84 coordinate reference system (EPSG:4326). The final set of environmental variables retained for each species is presented in Table 2.

Table 2. Environmental variables selected for each species.

Species	Climate Variables	Topographic Variables	Soil Variables
<i>Q. acuta</i>	BIO1, BIO3, BIO6, BIO14		
<i>M. thunbergii</i>	BIO1, BIO3, BIO5, BIO6, BIO12	Altitude	pH
<i>Q. glauca</i>	BIO1, BIO5, BIO6, BIO14	TPI	Clay content
<i>C. sieboldii</i>	BIO1, BIO3, BIO6, BIO14, BIO15	TWI	

2.3. Species Distribution Modeling and Ensemble Framework

Species distribution models were constructed using the BIOMOD2 package in R (version 4.4.3) [20]. By jointly applying statistical and machine learning-based models, we sought to mutually complement the intrinsic characteristics and differing assumptions of each model and to ensure diversity in the ensemble predictions [17,21]; a total of 10 models were used: Generalized Linear Model (GLM), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Random Forest (RF), Multivariate Adaptive Regression Splines (MARS), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Artificial Neural Network (ANN), Extreme Gradient Boosting (XGBOOST), and Maximum Entropy (MAXNET). All individual models were run using the hyperparameter settings predefined in BIOMOD2 (the bigboss option), and the hyperparameter values applied to the main machine learning models (RF, GBM, ANN, XGBOOST) are summarized in Table S2. To ensure the reproducibility of the analysis, a fixed random seed was specified at each stage of pseudo-absence extraction, model training, and spatial projection. The versions of the main packages used in the analysis were as follows: BIOMOD2 (4.3.4.5), terra (1.9.11), randomForest (4.7-1.2), gbm (2.2.3), nnet (7.3-20), xgboost (3.2.1.1), earth (5.3.5), mda (0.5.5), rpart (4.1.24), mgcv (1.9.1), gam (1.22.7), and maxnet (0.1.4).

For model training, occurrence data consisted of species-specific occurrence points obtained from the 7th NFI and 5th NES data, while pseudo-absence data were randomly extracted from NFI survey sites where the presence of the target species had not been recorded. The ratio of presence to pseudo-absence data was set at 1:1 (prevalence = 0.5). This was because, for the machine learning and classification-based models that constitute the major portion of the ensemble in this study (RF, GBM, MARS, CTA, FDA, ANN, XGBOOST), using the same number of pseudo-absences as presences is recommended [39], and because doing so avoids extreme class imbalance in the present study, in which the number of occurrence points is limited. However, since a relatively large number of pseudo-absences can be advantageous for regression-based models (GLM, GAM), a total of 20 pseudo-absence sets were constructed to partially compensate for this, thereby reducing variability arising from the random extraction of pseudo-absences. For each set, the training and validation data were randomly split at a ratio of 80:20, and this splitting was repeated five times (five repeated random splits); model performance was evaluated using the AUC (Area Under the Receiver Operating Characteristic Curve) and the TSS (True Skill Statistic) [40,41]. Variable importance for each individual model was computed using the permutation-based method in BIOMOD2; permutation was repeated three times per model run, and values across the 20 pseudo-absence sets $\times$ 5 repeated random splits (100 model runs in total) were averaged to compare the relative contributions of the environmental variables.

The final potential distribution projections were derived using the Committee Averaging method. CA is an approach that converts the continuous suitability values produced by individual models into binary presence–absence outcomes according to a threshold criterion, and then overlays these to compute the level of agreement in presence predictions among the models [21,22]. In this study, the prediction of each individual model was binarized by applying the threshold that maximized its TSS [42], and only individual models with a performance of $TSS \geq 0.7$ were included in the ensemble [41,43]. Because

the ensemble result represents the level of agreement in presence predictions among the models, it was binarized by applying an agreement cutoff of 0.5—that is, the criterion that a majority of models predicted presence—after which the TSS of the ensemble model was computed. The overall workflow of the study is presented in Figure 2.

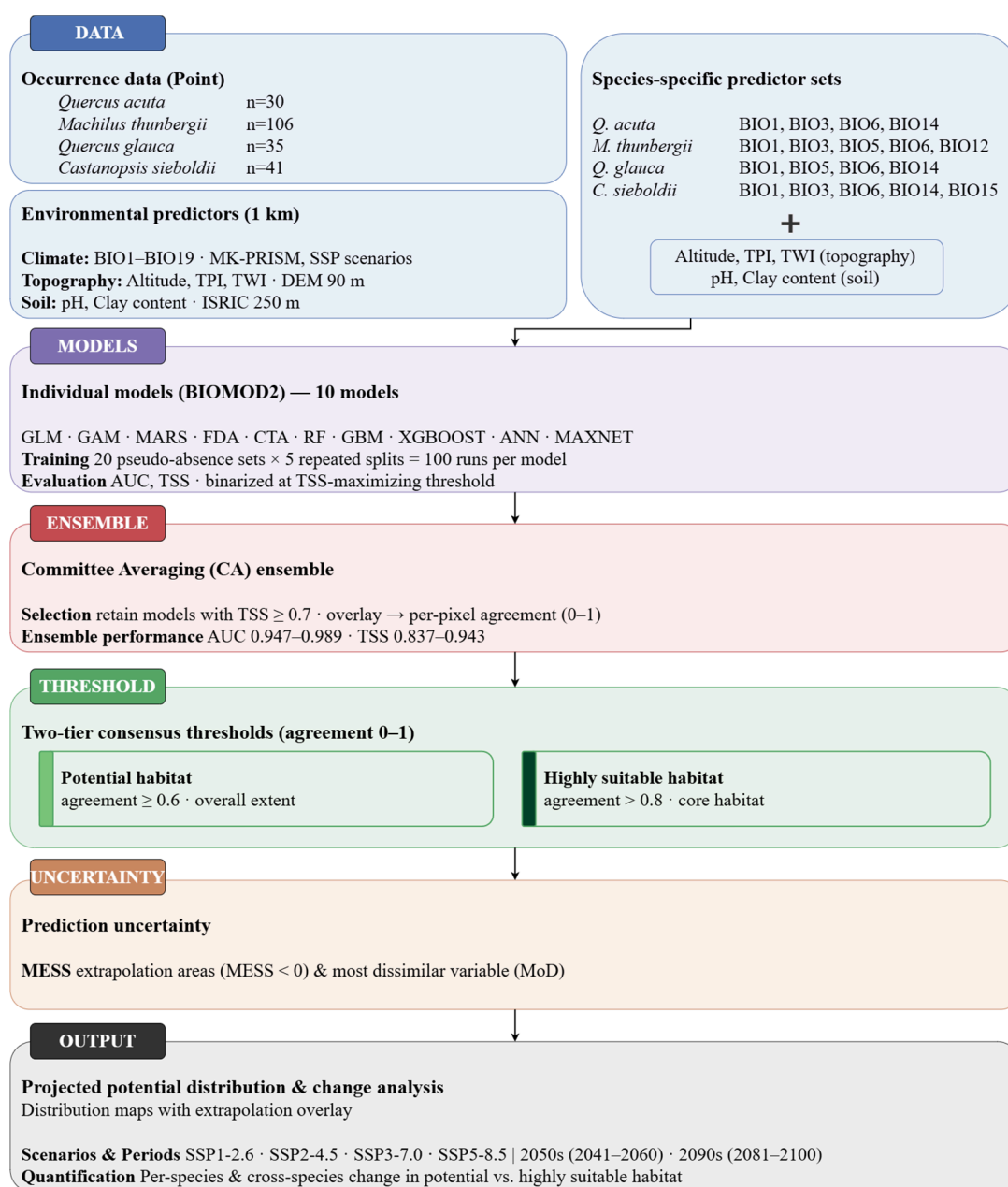


Figure 2. Overall workflow of the modeling framework used in this study.

2.4. Analysis of Changes in Potential Distribution

Based on the agreement values (0–1) produced by the CA ensemble models, a two-tier threshold was applied. Areas with an agreement of 0.6 or higher were defined as “potential habitat,” and areas exceeding 0.8 were defined as “highly suitable habitat.” In particular, highly suitable habitat corresponds to areas of high inter-model agreement, where most individual models consistently predicted presence. In this study, highly suitable habitat was regarded as the core area in which a species can be stably distributed even under climate change, and it was used as a reliable indicator for interpreting changes in potential distribution.

To evaluate the sensitivity of the results to threshold settings, all analyses were repeated using alternative threshold combinations—relaxed (0.5/0.7) and strict (0.65/0.85)—in addition to the baseline (0.6/0.8) (Table S1). The sensitivity analysis showed that the direction of change in potential habitat and the relative ranking among species were consistently maintained across all three combinations, confirming that the main conclusions of this study are robust to the choice of thresholds. However, because extreme criteria (relaxed or strict) may increase the sensitivity of interpretation by delineating habitat ranges as relatively broad or narrow, the intermediate baseline thresholds (0.6/0.8) were ultimately adopted in this analysis. The analysis of distribution changes under future climate scenarios was conducted for the four SSP scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) and two future periods (2050s and 2090s), through which changes in the area and spatial distribution of potential habitat and highly suitable habitat were projected.

2.5. Extrapolation Uncertainty Analysis

To quantify the predictive uncertainty associated with extrapolation into future climate conditions, a Multivariate Environmental Similarity Surface (MESS) analysis was performed [28]. MESS quantifies how similar the environmental conditions of each future climate grid cell are to the climate range used in model training; grid cells with negative values (<0) are identified as extrapolation areas, where one or more environmental variables fall outside the training range. In this study, along with the spatial distribution of MESS, the variable that deviated most from the training range in each extrapolation grid cell (the most dissimilar variable, MoD) was recorded to identify the main variables driving extrapolation for each species.

3. Results and Discussion

3.1. Model Performance and Effectiveness of the Ensemble Approach

The predictive performance of the 10 individual models and the CA ensemble model constructed for each species was evaluated based on AUC and TSS. The AUC of the individual models ranged from 0.782 to 0.990 across species, and the TSS ranged from 0.547 to 0.927. In particular, some statistical models (GLM, GAM) showed relatively low predictive performance, with TSS below 0.7 [40,41]. This performance variation among individual models, together with the variability across repeated runs, was mitigated through the ensemble technique. When only individual models with $TSS \geq 0.7$ were selected and combined using the CA method, the ensemble models yielded AUC values of 0.947–0.989 and TSS values of 0.837–0.943, showing higher predictive power and lower variability than the individual models (Table 3). Accordingly, the CA ensemble results were used to present the current and future potential distributions of each species in this study.

However, the high performance metrics obtained in this study need to be interpreted with caution. Because some species have a relatively small number of occurrence points (30–41) and are concentrated along the southern coast and on offshore islands, the resulting performance may have been partly influenced by the spatial clustering of occurrence points and the associated spatial autocorrelation. In particular, it is known that the smaller the sample size, the lower the reliability of predictive performance and the greater the variability [44]. Moreover, under conditions of limited samples, machine learning-based models with high degrees of freedom are prone to overfitting, whereas statistical models with simpler structures are known to carry a relatively lower risk of it [45].

To examine this concern, we evaluated how similar the predictions of the statistical models (GLM, GAM), which have a relatively low risk of overfitting, were to the ensemble predictions. As a result, the predictions of the statistical models showed a high spatial rank correlation with the ensemble predictions for all species (Spearman $\rho = 0.82$ – 0.94),

a level comparable to or even higher than that of the machine learning-based models (Table S3). This suggests that the spatial distribution patterns presented by the ensemble were not governed by the overfitting of any particular machine learning-based model, but were instead based on a consistent signal shared across the statistical models as well. Nevertheless, the uncertainty arising from the spatial bias of the occurrence data is difficult to rule out entirely, and this is a factor that should be considered when interpreting the results of this study. The predictive performance of each individual model and its frequency of inclusion in the ensemble are presented in Table S4.

Table 3. Predictive performance (mean $\pm$ SD) of individual models and the Committee Averaging (CA) ensemble for each species.

Model	<i>Q. acuta</i>		<i>M. thunbergii</i>		<i>Q. glauca</i>		<i>C. sieboldii</i>	
	AUC	TSS	AUC	TSS	AUC	TSS	AUC	TSS
GLM	0.834 $\pm$ 0.121	0.640 $\pm$ 0.244	0.921 $\pm$ 0.054	0.791 $\pm$ 0.102	0.782 $\pm$ 0.127	0.547 $\pm$ 0.253	0.880 $\pm$ 0.108	0.739 $\pm$ 0.219
GAM	0.865 $\pm$ 0.107	0.697 $\pm$ 0.219	0.908 $\pm$ 0.053	0.789 $\pm$ 0.111	0.819 $\pm$ 0.106	0.610 $\pm$ 0.219	0.897 $\pm$ 0.087	0.767 $\pm$ 0.187
MARS	0.905 $\pm$ 0.093	0.780 $\pm$ 0.182	0.954 $\pm$ 0.039	0.829 $\pm$ 0.091	0.894 $\pm$ 0.120	0.706 $\pm$ 0.245	0.949 $\pm$ 0.067	0.870 $\pm$ 0.156
FDA	0.952 $\pm$ 0.065	0.862 $\pm$ 0.150	0.963 $\pm$ 0.030	0.856 $\pm$ 0.086	0.897 $\pm$ 0.102	0.703 $\pm$ 0.227	0.960 $\pm$ 0.070	0.896 $\pm$ 0.150
CTA	0.931 $\pm$ 0.068	0.847 $\pm$ 0.169	0.917 $\pm$ 0.047	0.812 $\pm$ 0.090	0.871 $\pm$ 0.098	0.731 $\pm$ 0.194	0.967 $\pm$ 0.053	0.927 $\pm$ 0.111
ANN	0.958 $\pm$ 0.060	0.855 $\pm$ 0.160	0.965 $\pm$ 0.026	0.822 $\pm$ 0.089	0.921 $\pm$ 0.077	0.686 $\pm$ 0.223	0.975 $\pm$ 0.046	0.856 $\pm$ 0.168
MAXNET	0.965 $\pm$ 0.059	0.833 $\pm$ 0.157	0.971 $\pm$ 0.026	0.840 $\pm$ 0.084	0.932 $\pm$ 0.076	0.758 $\pm$ 0.197	0.990 $\pm$ 0.027	0.915 $\pm$ 0.106
GBM	0.970 $\pm$ 0.055	0.855 $\pm$ 0.151	0.969 $\pm$ 0.030	0.848 $\pm$ 0.078	0.917 $\pm$ 0.082	0.728 $\pm$ 0.192	0.988 $\pm$ 0.029	0.916 $\pm$ 0.119
RF	0.973 $\pm$ 0.056	0.828 $\pm$ 0.172	0.969 $\pm$ 0.027	0.825 $\pm$ 0.086	0.924 $\pm$ 0.076	0.718 $\pm$ 0.206	0.989 $\pm$ 0.030	0.897 $\pm$ 0.117
XGBOOST	0.952 $\pm$ 0.078	0.835 $\pm$ 0.187	0.959 $\pm$ 0.034	0.822 $\pm$ 0.090	0.901 $\pm$ 0.092	0.706 $\pm$ 0.202	0.972 $\pm$ 0.049	0.900 $\pm$ 0.120
CA ensemble	0.983 $\pm$ 0.033	0.914 $\pm$ 0.084	0.968 $\pm$ 0.027	0.867 $\pm$ 0.074	0.947 $\pm$ 0.049	0.837 $\pm$ 0.107	0.989 $\pm$ 0.026	0.943 $\pm$ 0.078

Note: Values are presented as mean $\pm$ SD (standard deviation) of 100 runs per cell, derived from 20 pseudo-absence sets $\times$ 5 repeated random splits. AUC, Area Under the Receiver Operating Characteristic Curve; TSS, True Skill Statistic; CA, Committee Averaging.

3.2. Variable Importance by Species

Comparison of the relative contributions of environmental variables revealed that BIO6 (minimum temperature of the coldest month) showed the highest variable importance for all four species, with mean importance values of 0.685 for *Q. acuta*, 0.800 for *M. thunbergii*, 0.523 for *Q. glauca*, and 0.498 for *C. sieboldii* (Table 4). The consistent dominance of BIO6 across all four species is in agreement with previous studies indicating that evergreen broad-leaved trees, which retain their leaves throughout winter, are particularly vulnerable to low-temperature stress, and that their distributions are closely linked to winter low-temperature conditions [9,26,46].

Beyond BIO6, the composition of the next most important variables differed among species. For *Q. acuta*, *M. thunbergii*, and *Q. glauca*, BIO1 (annual mean temperature) ranked second, followed by BIO14 (precipitation of the driest month) in *Q. acuta* and *Q. glauca*, and by BIO5 (maximum temperature of the warmest month) in *M. thunbergii*. In contrast, *C. sieboldii* showed BIO15 (precipitation seasonality) as a top contributing variable, which was not selected for any of the other species. These differences in variable composition indicate that, even within the same warm-temperate taxonomic group, the key environmental variables driving species distributions can vary among species [24], and they suggest that future responses to the same SSP scenario may also differ among species.

The relative contributions of topographic and soil variables were consistently lower than those of climatic variables across all four species. Among the topographic variables, altitude showed comparatively higher values, ranging from 0.064 to 0.082, while TPI and TWI were below 0.05 in all species. The soil variables—pH and clay content—also ranged from 0.02 to 0.06. These results are consistent with previous studies suggesting that climatic factors are the primary determinants of plant distributions in species distribution models,

whereas the influence of topographic and soil conditions tends to become more pronounced at finer spatial scales [47].

Table 4. Mean variable importance of environmental variables for each species.

Variable		Species			
		<i>Q. acuta</i>	<i>M. thunbergii</i>	<i>Q. glauca</i>	<i>C. sieboldii</i>
Climate	BIO1	0.105	0.133	0.191	0.107
	BIO3	0.088	0.046	–	0.083
	BIO5	–	0.120	0.091	–
	BIO6	0.685	0.800	0.523	0.498
	BIO12	–	0.061	–	–
	BIO14	0.100	–	0.184	0.085
	BIO15	–	–	–	0.290
Topography	Altitude	0.068	0.064	0.082	0.065
	TPI	0.031	0.023	0.039	0.021
	TWI	0.031	0.025	0.047	0.022
Soil	pH	0.040	0.017	0.059	0.032
	Clay content	0.041	0.022	0.047	0.042

Note: Values represent the mean variable importance averaged across 10 models $\times$ 100 runs per model (20 pseudo-absence sets $\times$ 5 repeated random splits) for each species. Dashes (–) indicate variables not included in the final model for the corresponding species based on the variable selection process described in Section 2.2.

3.3. Species-Specific Changes in Potential Distribution

3.3.1. *Quercus acuta*

Under the current period (2000–2019), the potential habitat of *Q. acuta* was confined to Jeju Island, the islands off the southern coast, and part of the southern east coast, and its highly suitable habitat was likewise centered on Jeju Island and the southern-coast islands (Table S5, Figure 3a). Under future climate change scenarios, potential habitat generally expanded around the existing distribution, and this tendency became more pronounced under the high-emission scenarios and toward the later period (2090s) (Figure 3). Although the change in potential habitat area was not consistent across scenarios and the maximum values of the two indicators (potential habitat and highly suitable habitat) did not occur under the same scenario, the spatial position of the highly suitable habitat, which has high model agreement, showed a consistent northward trend from the southern coast along the east coast to the Yeongdong region of Gangwon across all scenarios (Figure 3). These results show that, in understanding the future distribution dynamics of *Q. acuta*, it is necessary to consider both the change in potential habitat area and the spatial shift in the highly suitable habitat simultaneously.

This northward trend is explained by the results of the variable importance analysis. The variable that contributed most to the distribution of *Q. acuta* was BIO6 (minimum temperature of the coldest month) (Table 4). This is consistent with previous studies indicating that the northern distribution of evergreen oaks (*Cyclobalanopsis*) is governed primarily by the minimum temperature of the coldest month [48]. Because *Q. acuta* must retain its evergreen leaves through winter, it is directly exposed to cold-induced damage to leaves and vascular tissue, and it is particularly vulnerable to freezing injury at the seedling stage, so that winter low temperatures act as a major bottleneck for establishment [49]. Indeed, the threshold of the minimum temperature of the coldest month governing its distribution has been reported to be about -4.7 °C [50], placing *Q. acuta* among the more cold-sensitive of the study species. Because BIO6 is projected to rise markedly relative to the present under all scenarios and periods (Table S7), this easing of the winter low-temperature constraint

is judged to be the main factor driving the expansion of the potential habitat and the northward shift in the highly suitable habitat. Meanwhile, the contraction of the highly suitable habitat in the southern region under the high-emission scenario (SSP5-8.5 2090s) can be interpreted in relation to changes in the second-ranked contributing variable, BIO14 (precipitation of the driest month). BIO14 increases relative to the present under SSP3-7.0 2090s, whereas under SSP5-8.5 2090s it remains at the present level (Table S7), indicating that the water supply corresponding to the temperature rise is not expected to be accompanied. Unlike deciduous trees, evergreen broad-leaved trees retain their leaves through winter and the dry season, so their water demand from transpiration persists; therefore, under conditions where evapotranspiration demand increases with rising temperature, they are prone to water deficit if dry-season precipitation is not sustained [51]. Accordingly, the highly suitable habitat of *Q. acuta* appears to have been redistributed toward the east coast, where dry-season moisture conditions are relatively favorable, suggesting that under intensifying warming the distribution of this species may also be constrained by dry-season precipitation.

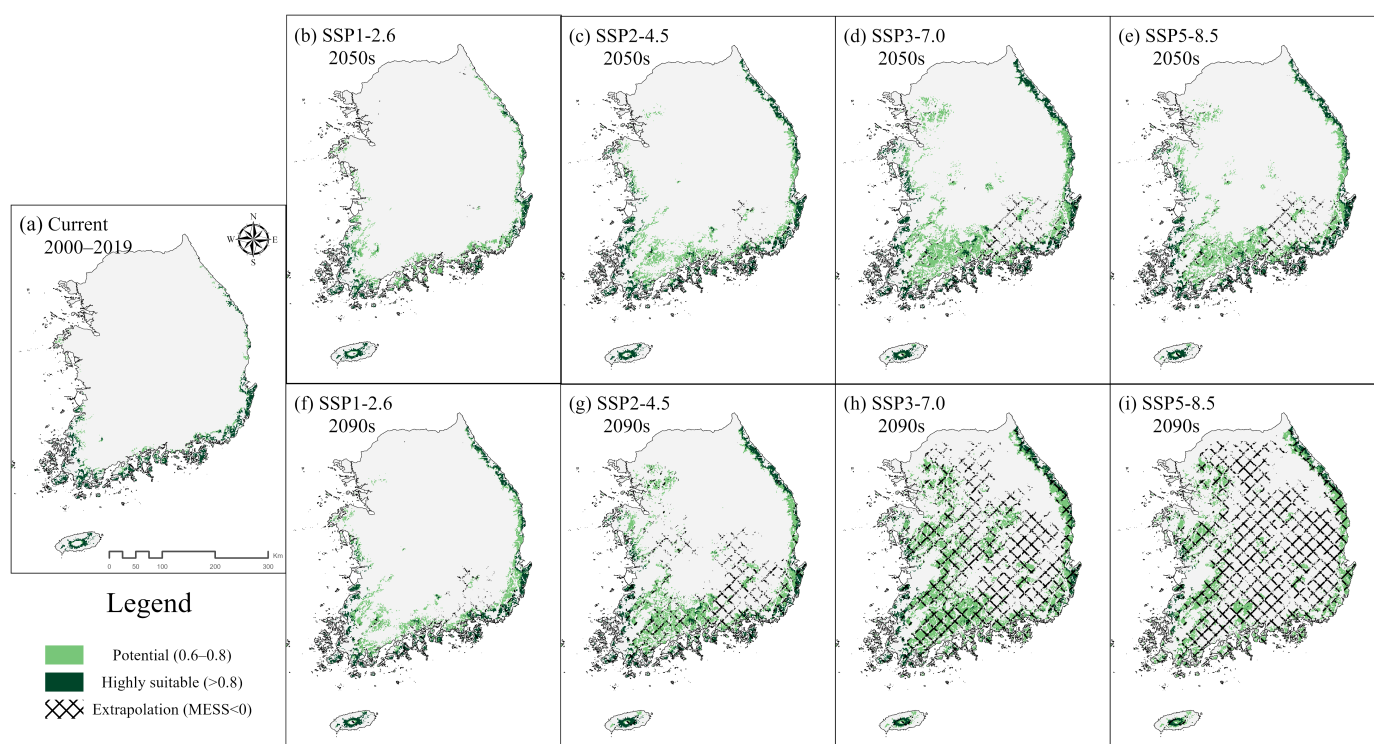


Figure 3. Current and projected potential distribution of *Quercus acuta* under climate change scenarios. (a) Current (2000–2019), (b–e) 2050s and (f–i) 2090s under SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5. Light green indicates potential habitat (agreement 0.6–0.8), dark green indicates highly suitable habitat (agreement > 0.8), and cross-hatching denotes extrapolation areas (MESS < 0). The 2050s and 2090s represent 2041–2060 and 2081–2100, respectively.

However, these future distribution projections need to be interpreted in light of the degree of extrapolation. The MESS analysis showed that under the low-emission, near-future conditions (SSP1-2.6 and SSP2-4.5 2050s), the extrapolation areas accounted for 6% or less of the total, indicating relatively high predictive reliability, whereas under the high-emission, later-period conditions the extrapolation areas increased sharply, reaching 68.5% under SSP3-7.0 2090s and 81.3% under SSP5-8.5 2090s (Table S6, Figure 3). This extrapolation arose mainly from the annual mean temperature (BIO1) falling outside the range of the training data (Table S6). In fact, future BIO1 is projected to rise by up to 6.5 °C relative to the present (Table S7), greatly exceeding the climatic range on which the model

was trained. Therefore, because the results for the high-emission, later-period scenarios, which projected an inland expansion of *Q. acuta*, correspond largely to extrapolation areas, it is reasonable to interpret them conservatively rather than to conclude that an actual range expansion will occur.

3.3.2. *Machilus thunbergii*

Under the current period (2000–2019), the potential habitat of *M. thunbergii* was mainly confined to the islands off the southern coast, and its highly suitable habitat was likewise centered on the southern-coast islands (Table S5, Figure 4a). Under future climate change scenarios, the potential habitat expanded around the existing distribution and, as in *Q. acuta*, this tendency became more pronounced under the high-emission scenarios and toward the later period (2090s), reaching its maximum area under SSP5-8.5 2090s (Table S5, Figure 4). In contrast, the highly suitable habitat area peaked under SSP3-7.0 2050s and then decreased under the high-emission, later-period conditions, contracting to a level similar to the present under SSP5-8.5 2090s (Table S5). As a result, the maximum values of the two indicators (potential habitat and highly suitable habitat) did not occur under the same scenario, and the pattern of area change was also inconsistent across scenarios. In contrast, the spatial position of the highly suitable habitat, which has high model agreement, showed a consistent northward trend from the southern coast along the east coast to the Yeongdong region of Gangwon across all scenarios (Figure 4). As observed for *Q. acuta*, this shows that in understanding the future distribution dynamics of *M. thunbergii*, it is necessary to consider both the change in potential habitat area and the spatial shift in the highly suitable habitat simultaneously.

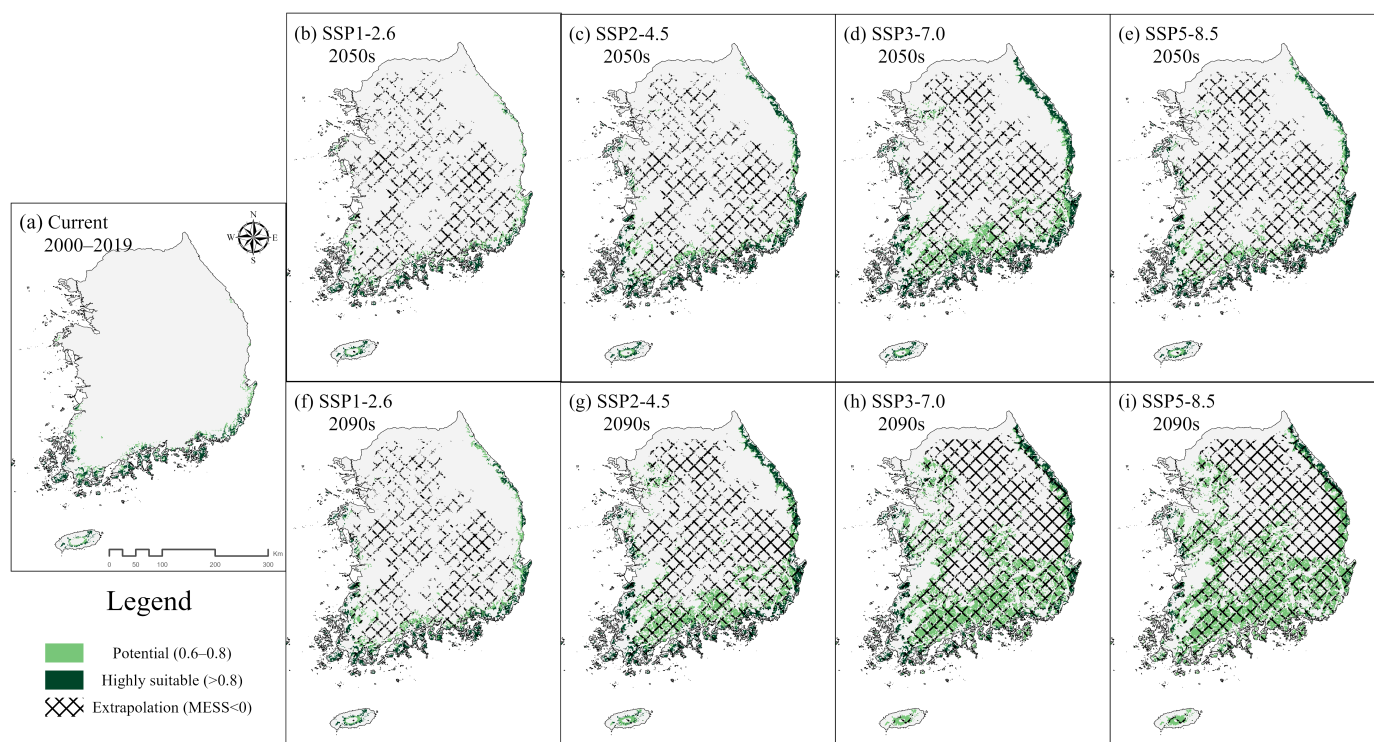


Figure 4. Current and projected potential distribution of *Machilus thunbergii* under climate change scenarios. (a) Current (2000–2019), (b–e) 2050s and (f–i) 2090s under SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5. Light green indicates potential habitat (agreement 0.6–0.8), dark green indicates highly suitable habitat (agreement > 0.8), and cross-hatching denotes extrapolation areas (MESS < 0). The 2050s and 2090s represent 2041–2060 and 2081–2100, respectively.

This pattern of distributional change is explained by the results of the variable importance analysis. The variable that contributed most to the distribution of *M. thunbergii* was BIO6 (minimum temperature of the coldest month), and its contribution was the highest among the four study species, indicating that the distribution of *M. thunbergii* responds most sensitively to winter low temperatures (Table 4). Indeed, together with the evergreen oaks, *M. thunbergii* is a representative warm-temperate evergreen broad-leaved tree whose distribution is governed by the minimum temperature of the coldest month [23], and in low-temperature treatment experiments, cellular damage has been reported to increase sharply at around $-8.1\text{ }^{\circ}\text{C}$, placing it among the species group sensitive to winter low temperatures [52]. Because BIO6 is projected to rise markedly relative to the present under all scenarios and periods (Table S7), the easing of the winter low-temperature constraint is judged to have driven the expansion of the potential habitat and a northward shift in highly suitable habitat. This strong dependence on low temperature is consistent with the result that *M. thunbergii* continues to expand its potential habitat even under the most extreme emission scenario (SSP5-8.5 2090s). Meanwhile, the result that the highly suitable habitat contracted to the present level even though the potential habitat expanded to its maximum under the same scenario cannot be explained by BIO6 alone and can be interpreted in relation to changes in the second-ranked contributing variable, BIO5 (maximum temperature of the warmest month). *M. thunbergii* is originally a species that prefers warm and humid climates [53], and under conditions of intensifying summer high temperatures its growth may be constrained through increased transpiration demand and reduced photosynthetic efficiency. Because BIO5 is projected to rise substantially under high-emission, later-period conditions (Table S7), it is judged that while the overall distributional range expanded owing to the easing of winter low temperatures, intensifying summer heat stress constrained the maintenance of the core habitat. Accordingly, the highly suitable habitat of *M. thunbergii* appears to have been redistributed toward the east coast, where the magnitude of summer temperature rise is relatively small, suggesting that the distribution of this species may be constrained not only by winter low temperatures but also, under intensifying warming, by summer high temperatures.

However, these future distribution projections need to be interpreted in light of the degree of extrapolation. The extrapolation pattern of *M. thunbergii* contrasts sharply with that of *Q. acuta* analyzed above. Unlike the extrapolation of *Q. acuta*, which increased sharply only under the high-emission, later-period conditions, that of *M. thunbergii* already reached about 43% of the total even under the low-emission, near-future condition (SSP1-2.6 2050s), exceeded 50% from SSP2-4.5 onward, and surpassed 90% under the high-emission, later-period conditions (SSP3-7.0 and SSP5-8.5 2090s) (Table S6, Figure 4). This extrapolation arose mainly from the maximum temperature of the warmest month (BIO5) falling outside the range of the training data (Table S6). The fact that the variable driving contraction of the highly suitable habitat and the variable driving extrapolation were both BIO5 consistently indicates that summer high-temperature conditions are a key source of uncertainty in future distribution projections for *M. thunbergii*. In fact, on the future distribution maps, a substantial portion of the inland-expanded potential habitat overlapped with extrapolation areas (Figure 4). Therefore, unlike *Q. acuta*, future distribution projections for *M. thunbergii* need to be interpreted conservatively across all scenarios, including the low-emission scenario.

3.3.3. *Quercus glauca*

Under the current period (2000–2019), the potential habitat of *Q. glauca* was mainly distributed across the islands off the southern coast and the southern part of the east coast, and its highly suitable habitat was likewise centered on the southern-coast islands

(Table S5, Figure 5a). Under future climate change scenarios, potential habitat expanded around the existing distribution, and, as in the two preceding species, this tendency became more pronounced under the high-emission scenarios and toward the later period (2090s) (Figure 5). However, unlike *Q. acuta* and *M. thunbergii*, *Q. glauca* showed a pattern in which the potential habitat and the highly suitable habitat expanded together. The maximum potential habitat area was obtained under SSP5-8.5 2090s, and the maximum highly suitable habitat area under SSP3-7.0 2090s, so the maximum values of the two indicators did not occur under the same scenario; nevertheless, the direction of change across scenarios and periods was more consistent than in *Q. acuta* and *M. thunbergii*, and the two indicators increased together at similar rates (Table S5). Spatially, highly suitable habitat shifted northward along the expansion extent of the potential habitat, across the southern region as a whole and along the east coast to the Yeongdong region of Gangwon (Figure 5). In this way, in contrast to *Q. acuta* and *M. thunbergii*, in which the expansion of the potential habitat and the change in the highly suitable habitat diverged, *Q. glauca* exhibited a tendency for area expansion to be accompanied by an increase in core habitat, and it was projected to have the largest expansion of potential distribution among the warm-temperate species analyzed in this study.

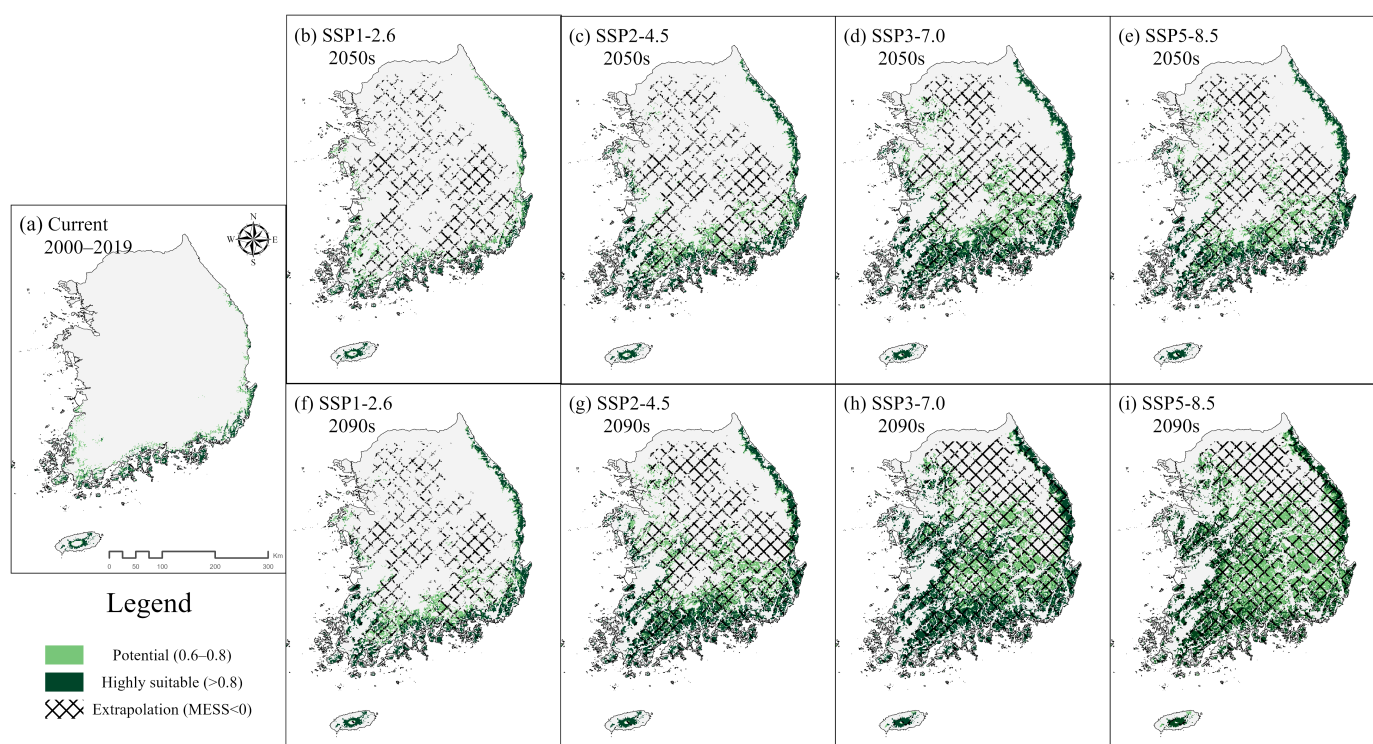


Figure 5. Current and projected potential distribution of *Quercus glauca* under climate change scenarios. (a) Current (2000–2019), (b–e) 2050s and (f–i) 2090s under SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5. Light green indicates potential habitat (agreement 0.6–0.8), dark green indicates highly suitable habitat (agreement > 0.8), and cross-hatching denotes extrapolation areas (MESS < 0). The 2050s and 2090s represent 2041–2060 and 2081–2100, respectively.

This pattern of distributional change is explained by the results of the variable importance analysis. In *Q. glauca* as well, BIO6 (minimum temperature of the coldest month) was identified as the top contributing variable (Table 4), but its contribution was lower than in *Q. acuta* and *M. thunbergii*, and BIO1 (annual mean temperature) and BIO14 (precipitation of the driest month) showed similar contributions as the next most important variables. This low dependence on low temperature is consistent with empirical evidence that *Q. glauca* has relatively high cold tolerance. In low-temperature treatment experiments,

the cold-tolerance limit of *Q. glauca* was reported to be about $-8.7\text{ }^{\circ}\text{C}$, enduring lower temperatures than *M. thunbergii* (about $-8.1\text{ }^{\circ}\text{C}$) [52], and in seedling overwintering experiments, *Q. glauca* maintained a lower mortality rate and more stable photosynthesis and carbohydrate metabolism than *Q. acuta*, showing greater tolerance to winter low temperatures than *Q. acuta* [49]. Because the constraint imposed by winter low temperatures on the distribution of *Q. glauca* is relatively small, its distribution is judged to be determined by the combined action of annual mean temperature conditions and dry-season water availability rather than by low temperature alone, requiring the simultaneous satisfaction of multiple environmental variables. Indeed, in the evergreen oaks (*Cyclobalanopsis*) occurring in the East Asian summer monsoon zone, the distribution has been reported to be governed by precipitation in addition to temperature, with precipitation of the driest month (BIO14) in particular acting as a major variable for *Q. glauca* [48]. Under future scenarios, all three of these variables (BIO6, BIO1, and BIO14) changed consistently in directions favorable to distributional expansion. BIO6 and BIO1 rose continuously regardless of scenario and period, and BIO14 also increased relative to the present up to SSP3-7.0 2090s (Table S7). As the directions of change in the main variables were mutually consistent, suitable conditions were strengthened simultaneously, which is judged to have induced the joint expansion of potential habitat and highly suitable habitat. Meanwhile, the result that the highly suitable habitat decreased relative to SSP3-7.0 2090s even though the potential habitat expanded to its maximum under SSP5-8.5 2090s can be interpreted in terms of changes in BIO14. Under this scenario, BIO14 remained at the present level (Table S7), so the large temperature rise was not accompanied by a corresponding increase in dry-season water supply. Given that the distribution of *Q. glauca* is sensitive to dry-season precipitation [48], it is interpreted that while the peripheral areas where the occurrence threshold is met by temperature rise alone expanded further, the expansion of the highly suitable areas, which require the simultaneous satisfaction of multiple environmental variables, was limited by the stagnation of dry-season water supply.

However, these future distribution projections need to be interpreted in light of the degree of extrapolation. Similar to *M. thunbergii*, the extrapolation of *Q. glauca* already reached about 43% of the total even under the low-emission, near-future condition (SSP1-2.6 2050s), exceeded 50% from SSP2-4.5 onward, and surpassed 90% under the high-emission, later-period conditions (SSP3-7.0 and SSP5-8.5 2090s) (Table S6, Figure 5). This extrapolation arose mainly from the maximum temperature of the warmest month (BIO5) falling outside the range of the training data (Table S6). It is particularly noteworthy that *Q. glauca* was the species projected to have the largest expansion of potential distribution in this study while at the same time being one of the species with the highest extrapolation proportion across all scenarios. In fact, on the future distribution maps, a substantial portion of the potential and highly suitable habitats that expanded into the inland and Gangwon regions overlapped with extrapolation areas (Figure 5). Therefore, because the large-scale distributional expansion projected for *Q. glauca* reflects a real climatic signal—the easing of the winter low-temperature constraint—while also arising substantially from extrapolation beyond the training range, it is reasonable to interpret the magnitude of that expansion conservatively rather than to conclude that an actual range expansion will occur.

3.3.4. *Castanopsis sieboldii*

Under the current period (2000–2019), the potential habitat of *C. sieboldii* was the narrowest among the four species analyzed in this study, being confined mainly to Jeju Island and the islands off the southern coast, and its highly suitable habitat was likewise centered on this region (Table S5, Figure 6a). Under the future climate change scenarios, *C. sieboldii* showed a pattern opposite to that of the three warm-temperate species analyzed

above. The potential habitat decreased relative to the present under all scenarios except SSP2-4.5 2090s, and the highly suitable habitat decreased under all scenarios; in particular, the contraction of the highly suitable habitat became more pronounced under the high-emission scenarios and toward the later period (2090s), being greatest under SSP5-8.5 2090s (Table S5, Figure 6). Unlike the northward trend of the highly suitable habitat observed in the other species, the highly suitable habitat of *C. sieboldii* did not shift northward spatially but contracted gradually within its existing distribution on Jeju Island and the southern-coast islands, and under the high-emission, later-period conditions the highly suitable area of its core distribution was projected to be almost lost (Figure 6). These results show that even species belonging to the same warm-temperate evergreen broad-leaved forest community can respond in opposite ways to future climate, and that the core distribution of *C. sieboldii* is highly likely to contract under future climate change conditions.

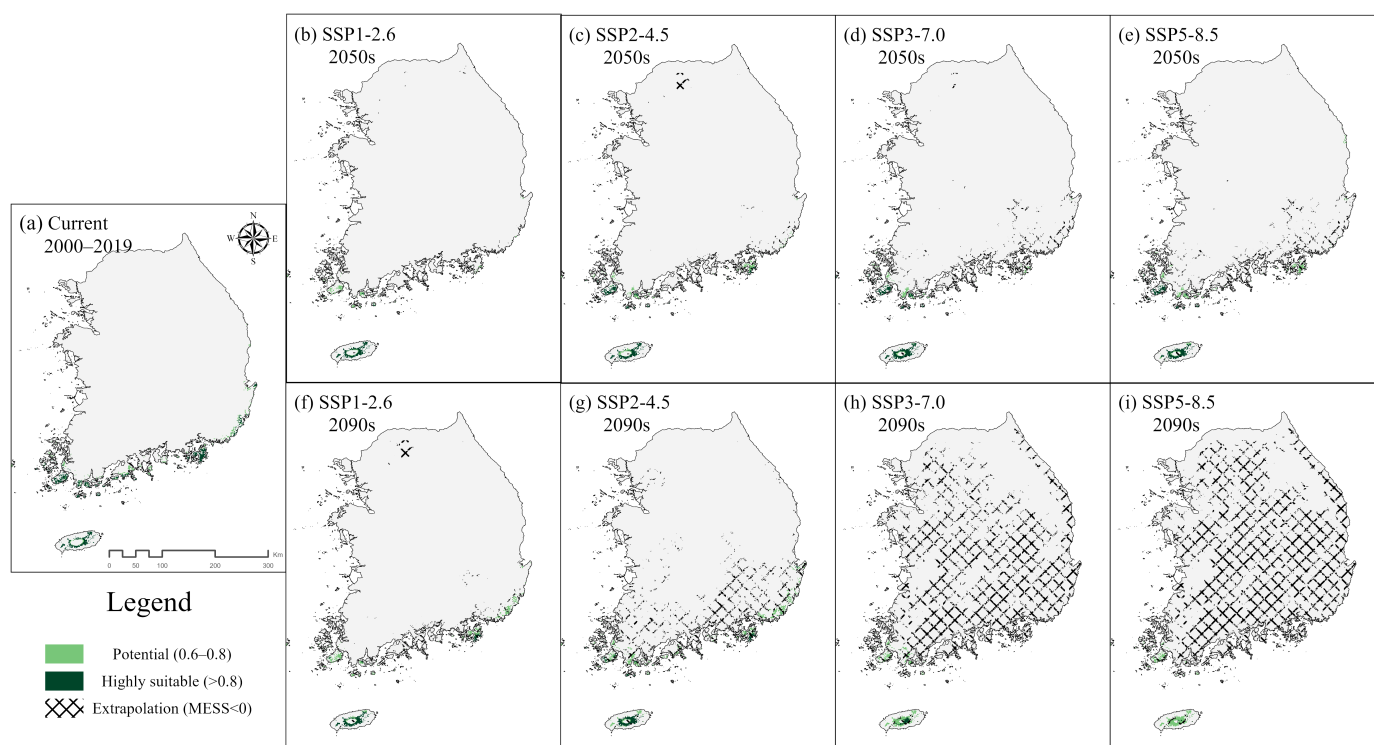


Figure 6. Current and projected potential distribution of *Castanopsis sieboldii* under climate change scenarios. (a) Current (2000–2019), (b–e) 2050s and (f–i) 2090s under SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5. Light green indicates potential habitat (agreement 0.6–0.8), dark green indicates highly suitable habitat (agreement > 0.8), and cross-hatching denotes extrapolation areas (MESS < 0). The 2050s and 2090s represent 2041–2060 and 2081–2100, respectively.

This pattern of distributional change is explained by the results of the variable importance analysis. The variable that contributed most to the distribution of *C. sieboldii* was BIO6 (minimum temperature of the coldest month), but its contribution was the lowest among the four study species (Table 4). This low dependence on winter low temperature suggests that, unlike the other three species in which the easing of the low-temperature constraint led directly to distributional expansion, warming alone is unlikely to expand the distribution of *C. sieboldii*. Indeed, in a study of evergreen broad-leaved tree species across the Taiwan–Japan archipelago, even as the overall potential habitat was projected to increase, *C. sieboldii*—an evergreen broad-leaved species dominant in the same warm-temperate zone—was predicted to lose about 38% of its potential habitat in the Ryukyu Islands, its southern range limit, by the 2080s, indicating vulnerability to climate change at the southern edge of its range [54]. This supports the possibility that temperature rise does not act

as a unilateral expansion factor for this species. Meanwhile, the second-ranked variable, BIO15 (precipitation seasonality), was selected as a major variable only in *C. sieboldii* among the four species; because BIO15 has been reported to be one of the main climatic variables governing the distribution of the genus *Castanopsis* in East Asia [55], this suggests that the suitable conditions for this species may be sensitive to the seasonal distribution of precipitation. However, under the future scenarios, BIO15 changed inconsistently, with increases and decreases diverging across scenarios and periods (Table S7). Taken together, it is judged that the limited expansion potential implied by the low contribution of BIO6 and the difficulty of maintaining suitable conditions due to the inconsistent variation in BIO15 acted in combination, so that the potential distribution of *C. sieboldii* contracted differently across scenarios without a consistent trend.

These future distribution projections need to be interpreted in light of the degree of extrapolation. Similar to *Q. acuta*, the extrapolation of *C. sieboldii* remained low, at 7% or less of the total under the low-emission, near-future conditions, and then increased sharply under the high-emission, later-period conditions, reaching 58.6% under SSP3-7.0 2090s and 74.9% under SSP5-8.5 2090s (Table S6, Figure 6); this extrapolation arose mainly from the annual mean temperature (BIO1) falling outside the range of the training data (Table S6). However, whereas these extrapolation areas are located mainly in the inland region, where the species was projected not to occur, the key result for this species—the contraction of the highly suitable habitat—occurred within the existing distribution, such as Jeju Island and the southern-coast islands, where training data were sufficiently available (Figure 6). Therefore, unlike the three preceding species, in which the expansion overlapped with extrapolation areas and thus required cautious interpretation, the contraction of the core habitat projected for *C. sieboldii* is judged to be a robust result relatively little affected by extrapolation, supporting the interpretation that this species will be vulnerable to future climate change. This is also consistent with previous studies projecting that the genus *Castanopsis* in East Asia will undergo distributional contraction in the future owing to warming and limited dispersal ability [55,56].

3.4. Implications

In this study, *Q. acuta*, *M. thunbergii*, and *Q. glauca* showed expansion of their potential habitat under all SSP scenarios, with their highly suitable habitat shifting northward into the central and Gangwon regions, whereas *C. sieboldii* showed contraction of both habitat types under most scenarios. The emergence of such opposite responses—expansion versus contraction—among species belonging to the same warm-temperate evergreen broad-leaved forest community shows that, even for climate change in the same direction (warming), differences in species-specific ecological requirements can lead to divergent distributional responses. Unlike the species in which relatively low winter cold tolerance means that the easing of the low-temperature constraint leads directly to distributional expansion (*Q. acuta*, *M. thunbergii*, and *Q. glauca*), *C. sieboldii* has a low dependence on low temperature and is sensitive to the seasonal distribution of precipitation, so that warming does not necessarily lead to distributional expansion. This suggests that changes in the distribution of warm-temperate tree species under climate change are difficult to generalize at the level of the vegetation zone, and that the establishment of forest conservation and adaptation strategies requires quantitative assessment reflecting species-specific changes in potential distribution [24].

Here, the reliability of the projections differs among species, so an asymmetric approach is required for their overall interpretation. Because the distributional expansion projected for the three species occurs largely in extrapolation areas, where the future climate falls outside the training range of the model, the magnitude of that expansion needs to

be interpreted with caution rather than concluded to be an actual range expansion; in particular, the species with the larger projected expansion of potential distribution tended to be the more strongly affected by extrapolation. In contrast, the contraction of the core habitat of *C. sieboldii* occurred within its existing distribution, where training data were sufficiently available, and is therefore relatively little affected by extrapolation, so it can be regarded as a more robust conclusion. In short, the results of this study indicate that the expansion potential of the three species can be interpreted with caution, whereas the vulnerability of *C. sieboldii* can be interpreted more clearly.

Meanwhile, such projected distributional changes do not imply an immediate reorganization of forest structure, because the actual range expansion of trees is constrained by seed dispersal ability and life-history traits. Oaks produce heavy nuts and depend mainly on animal-mediated dispersal by the Eurasian jay (*Garrulus glandarius*) and rodents [57,58], and for *M. thunbergii*, seed dispersal by birds is also known to be important [59,60]. The Eurasian jay transports acorns over mean distances of several tens of meters, up to a few hundred meters per event [58], and is reported to be potentially capable of dispersing them as far as about 4 km [61]. However, such long-distance dispersal is infrequent, and most dispersal remains at the scale of tens of meters; combined with the generation time required to reach establishment and maturity and with landscape fragmentation, it is difficult for dispersal to fully keep pace with spatial changes in potential suitable areas that shift on the scale of tens to hundreds of kilometers. Therefore, even if climatically suitable areas newly emerge, a considerable time lag is expected before actual colonization and establishment. Ultimately, whether warm-temperate tree species actually become established in the central and Gangwon regions must be judged by considering not only climatic suitability but also dispersal limitation and the time scale of succession.

When these predictive uncertainties and ecological constraints are considered together, the two-tier threshold scheme applied in this study, combined with extrapolation information, can be usefully employed to spatially operationalize climate-change-adaptive forest management. Specifically, among the highly suitable habitats with high inter-model agreement (>0.8), the areas judged to be based on a real climatic signal with little influence of extrapolation correspond to candidate sites where adaptive regeneration or supplementary planting of warm-temperate species can be considered as a priority; in such areas, actual vegetation change and early establishment can be tracked through high-resolution remote sensing and digital monitoring. In contrast, areas that are projected as potential habitat but have relatively low agreement ($0.6\text{--}0.8$), as well as expansion areas overlapping with extrapolation areas, are better designated as flexible management and monitoring zones where the progress of natural succession is observed first, rather than immediately applying large-scale artificial planting. Meanwhile, for species such as *C. sieboldii*, for which contraction of the core habitat within the existing native range is projected, an in situ conservation strategy centered on the current distribution—such as Jeju Island and the southern-coast islands—should take priority over management premised on northward expansion; to this end, the establishment of a forest protection system that includes detailed diagnosis of microclimate and stand structure, early stress detection, and genetic resource conservation is required. This approach of differentiating the intensity of management intervention according to the level of predictive reliability can contribute to the efficient allocation of limited resources by integrating predictive uncertainty into management decision-making.

4. Conclusions

This study applied a CA ensemble technique to *Q. acuta*, *M. thunbergii*, *Q. glauca*, and *C. sieboldii*, the major constituent species of warm-temperate evergreen broad-leaved forests

in South Korea, to project changes in their potential distributions under future climate conditions, and it quantitatively compared interspecific differences in response through a two-tier threshold scheme distinguishing potential habitat from highly suitable habitat. As a result, *Q. acuta*, *M. thunbergii*, and *Q. glauca* generally showed a tendency for the potential habitat to expand and the highly suitable habitat to shift northward, whereas *C. sieboldii* showed the opposite response, with both habitat types contracting under most scenarios. This shows that even species belonging to the same warm-temperate species group can respond differently to future climate, and that species-specific quantitative assessment can provide a more concrete basis for forest conservation and management decision-making than a generalized outlook at the level of the vegetation zone.

In addition, by evaluating projected distributional changes together with the degree of extrapolation, this study interpreted the results by distinguishing the level of reliability for each species. The distributional expansion projected for the three species increasingly appeared toward the high-emission, later-period scenarios, in extrapolation areas beyond the training range, requiring cautious interpretation, whereas the contraction of the core habitat of *C. sieboldii* occurred within its existing distribution, where the influence of extrapolation is small, and was thus judged to be a relatively robust result. In this way, the approach of this study—simultaneously assessing changes in potential distribution area and the spatial shift in climatically stable core habitat and further distinguishing the associated predictive uncertainty—can be used as a basis for differentiating the priority of management intervention according to the level of predictive reliability.

However, the projections of this study represent potential distributions based on climatic suitability, whereas the actual formation and maintenance of distributions are jointly influenced by seed dispersal ability, the time lag of succession, the spatial bias of occurrence data, and extrapolation into future climates. Therefore, future work needs to complement the ecological realism and applicability of the projections through dynamic models that integrate such dispersal and successional processes.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f17080993/s1>. Table S1: Sensitivity of projected habitat changes to the suitability thresholds; Table S2: Hyperparameter settings of the four machine learning algorithms (RF, GBM, ANN, and XGBOOST) used in the ensemble; Table S3: Spatial correlation between individual model predictions and the committee averaging (CA) ensemble prediction; Table S4: Predictive performance and ensemble selection frequency of each individual model by species; Table S5: Projected potential and highly suitable habitat area by species, scenario, and period; Table S6: Proportion of extrapolation areas and the main driving variable by species, scenario, and period; Table S7: Mean and standard deviation of bioclimatic variables across the forested study area under current and future SSP scenarios.

Author Contributions: J.-H.P.: conceptualization, methodology, formal analysis, visualization, project administration, writing—original draft. J.-G.L.: conceptualization, writing—original draft, writing—review and editing. H.D.S.: formal analysis, writing—review and editing. H.-J.L.: writing—review and editing. D.-H.L.: writing—review and editing. S.H.E.: writing—review and editing. H.-J.K.: conceptualization, funding acquisition, supervision, project administration, writing—review and editing. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by the “Development of Soil Information Maps and Estimation of Organic Carbon Stocks in Inland Wetlands” project (No. 2025-2134-01), funded by the Ministry of Environment, Republic of Korea.

Data Availability Statement: Species occurrence data from the 7th National Forest Inventory (Korea Forest Service) were used under authorization from the data provider and are not publicly available; access requests should be directed to the Korea Forest Service. Occurrence data from the 5th National

Ecosystem Survey (National Institute of Ecology, Republic of Korea) are publicly available. Climate data (MK-PRISM v2.1) for the current period and SSP-based projections for the future periods were obtained from the Korea Meteorological Administration. Soil data were obtained from the ISRIC SoilGrids database (data.isric.org). Topographic data (DEM 90 m) were obtained from the National Geographic Information Institute (www.ngii.go.kr). Code and processed datasets generated during the study are available from the corresponding author upon reasonable request.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. IPCC. *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*; Cambridge University Press: Cambridge, UK; New York, NY, USA, 2022. [CrossRef]
2. Keenan, R.J. Climate change impacts and adaptation in forest management: A review. *Ann. For. Sci.* **2015**, *72*, 145–167. [CrossRef]
3. Lim, C.-H.; Yoo, S.; Choi, Y.; Jeon, S.-W.; Son, Y.; Lee, W.-K. Assessing climate change impact on forest habitat suitability and diversity in the Korean Peninsula. *Forests* **2018**, *9*, 259. [CrossRef]
4. McDowell, N.G.; Allen, C.D.; Anderson-Teixeira, K.J.; Aukema, B.H.; Bond-Lamberty, B.; Chini, L.; Clark, J.S.; Dietze, M.; Grossiord, C.; Hanbury-Brown, A.; et al. Pervasive shifts in forest dynamics in a changing world. *Science* **2020**, *368*, eaaz9463. [CrossRef] [PubMed]
5. Ha, K.-J.; Heo, K.-Y.; Lee, S.-S.; Yun, K.-S.; Jhun, J.-G. Variability in the East Asian monsoon: A review. *Meteorol. Appl.* **2012**, *19*, 200–215. [CrossRef]
6. Yim, Y.-J.; Kira, T. Distribution of forest vegetation and climate in the Korean Peninsula. I. Distribution of some indices of thermal climate. *Jpn. J. Ecol.* **1975**, *25*, 77–88.
7. Pecchi, M.; Marchi, M.; Burton, V.; Giannetti, F.; Moriondo, M.; Bernetti, I.; Bindi, M.; Chirici, G. Species distribution modelling to support forest management. A literature review. *Ecol. Modell.* **2019**, *411*, 108817. [CrossRef]
8. Park, S.-G.; Choi, S.-H.; Lee, S.-C. A review of vegetation succession in warm-temperate evergreen broad-leaved forests. *Korean J. Environ. Ecol.* **2018**, *32*, 77–96. (In Korean) [CrossRef]
9. Sakai, A. Freezing tolerance of evergreen and deciduous broad-leaved trees in Japan with reference to tree regions. *Low Temp. Sci. Ser. B* **1979**, *36*, 1–19.
10. Yun, J.-H.; Nakao, K.; Park, C.-H.; Lee, B.-Y. Potential habitats and change prediction of *Machilus thunbergii* Siebold & Zucc. in Korea by climate change. *Korean J. Environ. Ecol.* **2011**, *25*, 903–910. (In Korean)
11. Eom, B.-C.; Kim, J.-W. A phytoclimatic review of warm-temperate vegetation zone of Korea. *Korean J. Ecol. Environ.* **2020**, *53*, 195–207. (In Korean) [CrossRef]
12. Jung, S.-Y.; Lee, K.-S.; Seol, A.; Lee, S.-G.; Lee, S.-B.; Kang, K.-S.; Kim, J.-S.; Choi, S.-Y.; Kim, W.-S.; Park, K.-E.; et al. *Customized Forest Stand Management and Resource Utilization Research for Major Warm-temperate Plantations*; Research Report No. 25-14; National Institute of Forest Science: Seoul, Republic of Korea, 2025; ISBN 979-11-6019-972-7. (In Korean)
13. Pearson, R.G.; Dawson, T.P. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **2003**, *12*, 361–371. [CrossRef]
14. Elith, J.; Leathwick, J.R. Species distribution models: Ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* **2009**, *40*, 677–697. [CrossRef]
15. Elith, J.; Graham, C.H.; Anderson, R.P.; Dudík, M.; Ferrier, S.; Guisan, A.; Hijmans, R.J.; Huettmann, F.; Leathwick, J.R.; Lehmann, A.; et al. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **2006**, *29*, 129–151. [CrossRef]
16. Araújo, M.B.; Whittaker, R.J.; Ladle, R.J.; Erhard, M. Reducing uncertainty in projections of extinction risk from climate change. *Glob. Ecol. Biogeogr.* **2005**, *14*, 529–538. [CrossRef]
17. Araújo, M.B.; New, M. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* **2007**, *22*, 42–47. [CrossRef] [PubMed]
18. Buisson, L.; Thuiller, W.; Casajus, N.; Lek, S.; Grenouillet, G. Uncertainty in ensemble forecasting of species distribution. *Glob. Change Biol.* **2010**, *16*, 1145–1157. [CrossRef]
19. Marmion, M.; Parviainen, M.; Luoto, M.; Heikkinen, R.K.; Thuiller, W. Evaluation of consensus methods in predictive species distribution modelling. *Divers. Distrib.* **2009**, *15*, 59–69. [CrossRef]
20. Thuiller, W.; Lafourcade, B.; Engler, R.; Araújo, M.B. BIOMOD—A platform for ensemble forecasting of species distributions. *Ecography* **2009**, *32*, 369–373. [CrossRef]
21. Hao, T.; Elith, J.; Guillera-Arroita, G.; Lahoz-Monfort, J.J. A review of evidence about use and performance of species distribution modelling ensembles like BIOMOD. *Divers. Distrib.* **2019**, *25*, 839–852. [CrossRef]
22. Meller, L.; Cabeza, M.; Pironon, S.; Barbet-Massin, M.; Maiorano, L.; Georges, D.; Thuiller, W. Ensemble distribution models in conservation prioritization: From consensus predictions to consensus reserve networks. *Divers. Distrib.* **2014**, *20*, 309–321. [CrossRef] [PubMed]

23. Park, S.-U.; Koo, K.-A.; Kong, W.-S. Potential impact of climate change on distribution of warm temperate evergreen broad-leaved trees in the Korean Peninsula. *J. Korean Geogr. Soc.* **2016**, *51*, 201–217. (In Korean) [[CrossRef](#)]
24. Koo, K.-A.; Park, S.-U.; Seo, C. Effects of climate change on the climatic niches of warm-adapted evergreen plants: Expansion or contraction? *Forests* **2017**, *8*, 500. [[CrossRef](#)]
25. Shin, M.-S.; Seo, C.; Park, S.-U.; Hong, S.-B.; Kim, J.-Y.; Jeon, J.-Y.; Lee, M. Prediction of potential habitat of Japanese evergreen oak (*Quercus acuta* Thunb.) considering dispersal ability under climate change. *J. Environ. Impact Assess.* **2018**, *27*, 291–306. (In Korean) [[CrossRef](#)]
26. Shin, S.; Kim, J.-H.; Kang, D.; Kim, J.-S.; Kang, H.-G.; Jang, H.-D.; Lee, J.; Han, J.-E.; Oh, H.-K. Northern distribution limits and future suitable habitats of warm temperate evergreen broad-leaved tree species designated as climate-sensitive biological indicator species in South Korea. *J. Ecol. Environ.* **2022**, *46*, 28. [[CrossRef](#)]
27. Lee, E.; Lee, J.; Seo, C. Habitat prediction of southern plants under SSP scenarios considering habitat climate characteristics. *J. Korean Soc. Environ. Restor. Technol.* **2024**, *27*, 179–195. (In Korean) [[CrossRef](#)]
28. Elith, J.; Kearney, M.; Phillips, S. The art of modelling range-shifting species. *Methods Ecol. Evol.* **2010**, *1*, 330–342. [[CrossRef](#)]
29. Korea Meteorological Administration (KMA). *Climatological Normals of Korea (1991–2020)*; Korea Meteorological Administration: Seoul, Republic of Korea, 2021. (In Korean)
30. Korea Forest Service (KFS). *Statistical Yearbook of Forestry*; Korea Forest Service: Daejeon, Republic of Korea, 2025. (In Korean)
31. Korea Forest Service (KFS). Forest Type Map (1:5000) [Dataset]. National Spatial Data Infrastructure Portal (VWorld). Available online: https://www.vworld.kr/dtmk/dtmk_ntads_s002.do?dsId=30136 (accessed on 1 August 2025). (In Korean)
32. IPCC. *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*; Cambridge University Press: Cambridge, UK; New York, NY, USA, 2021. [[CrossRef](#)]
33. Riahi, K.; van Vuuren, D.P.; Kriegler, E.; Edmonds, J.; O'Neill, B.C.; Fujimori, S.; Bauer, N.; Calvin, K.; Dellink, R.; Fricko, O.; et al. The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Glob. Environ. Change* **2017**, *42*, 153–168. [[CrossRef](#)]
34. Dormann, C.F.; Elith, J.; Bacher, S.; Buchmann, C.; Carl, G.; Carré, G.; Marquéz, J.R.G.; Gruber, B.; Lafourcade, B.; Leitão, P.J.; et al. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **2013**, *36*, 27–46. [[CrossRef](#)]
35. Moeslund, J.E.; Arge, L.; Bøcher, P.K.; Dalgaard, T.; Svenning, J.-C. Topography as a driver of local terrestrial vascular plant diversity patterns. *Nord. J. Bot.* **2013**, *31*, 129–144. [[CrossRef](#)]
36. Weiss, A. Topographic Position and Landforms Analysis. In Proceedings of the ESRI User Conference, San Diego, CA, USA, 9–13 July 2001.
37. Beven, K.J.; Kirkby, M.J. A physically based, variable contributing area model of basin hydrology. *Hydrol. Sci. Bull.* **1979**, *24*, 43–69. [[CrossRef](#)]
38. Rota, F.; Scherrer, D.; Bergamini, A.; Price, B.; Walther, L.; Baltensweiler, A. Unravelling the impact of soil data quality on species distribution models of temperate forest woody plants. *Sci. Total Environ.* **2024**, *944*, 173719. [[CrossRef](#)] [[PubMed](#)]
39. Barbet-Massin, M.; Jiguet, F.; Albert, C.H.; Thuiller, W. Selecting pseudo-absences for species distribution models: How, where and how many? *Methods Ecol. Evol.* **2012**, *3*, 327–338. [[CrossRef](#)]
40. Fielding, A.H.; Bell, J.F. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* **1997**, *24*, 38–49. [[CrossRef](#)]
41. Allouche, O.; Tsoar, A.; Kadmon, R. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* **2006**, *43*, 1223–1232. [[CrossRef](#)]
42. Liu, C.; Berry, P.M.; Dawson, T.P.; Pearson, R.G. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **2005**, *28*, 385–393. [[CrossRef](#)]
43. Franklin, J. *Mapping Species Distributions: Spatial Inference and Prediction*, 1st ed.; Cambridge University Press: Cambridge, UK, 2009; 320p.
44. Wisz, M.S.; Hijmans, R.J.; Li, J.; Peterson, A.T.; Graham, C.H.; Guisan, A. Effects of sample size on the performance of species distribution models. *Divers. Distrib.* **2008**, *14*, 763–773. [[CrossRef](#)]
45. Merow, C.; Smith, M.J.; Edwards, T.C.; Guisan, A.; McMahon, S.M.; Normand, S.; Thuiller, W.; Wüest, R.O.; Zimmermann, N.E.; Elith, J. What do we gain from simplicity versus complexity in species distribution models? *Ecography* **2014**, *37*, 1267–1281. [[CrossRef](#)]
46. Ge, J.; Xie, Z. Geographical and climatic gradients of evergreen versus deciduous broad-leaved tree species in subtropical China: Implications for the definition of the mixed forest. *Ecol. Evol.* **2017**, *7*, 3636–3644. [[CrossRef](#)] [[PubMed](#)]
47. Huang, E.; Chen, Y.; Yu, S. Climate factors drive plant distributions at higher taxonomic scales and larger spatial scales. *Front. Ecol. Evol.* **2024**, *11*, 1233936. [[CrossRef](#)]
48. Lin, L.; Jiang, X.L.; Guo, K.Q.; Byng, J.W.; Deng, M. Climate change impacts the distribution of *Quercus* section *Cyclobalanopsis* (Fagaceae), a keystone lineage in East Asian evergreen broadleaved forests. *Plant Divers.* **2023**, *45*, 552–568. [[CrossRef](#)] [[PubMed](#)]

49. Song, W.; Kim, S.; Lee, M.; Huh, W.; Kim, S.; Park, S.; Baek, J.; Park, Y.; Kim, K.; Park, C.; et al. Contrasting physiological strategies of *Quercus acuta* and *Q. glauca* half-sib families under differing winter thermal conditions. *Front. For. Glob. Change* **2026**, *9*, 1861793. [[CrossRef](#)]
50. Nakao, K.; Matsui, T.; Tanaka, N. Climatic controls of the distribution and abundance of two evergreen *Quercus* species in Japan. *Jpn. J. For. Environ.* **2009**, *51*, 27–37.
51. Ouyang, L.; Wu, J.; Zhao, P.; Li, Y.; Zhu, L.; Ni, G.; Rao, X. Consumption of precipitation by evapotranspiration indicates potential drought for broadleaved and coniferous plantations in hilly lands of South China. *Agric. Water Manag.* **2021**, *252*, 106920. [[CrossRef](#)]
52. Jin, E.-J.; Yoon, J.-H.; Bae, E.-J.; Choi, M.-S. Comparative assessment of cold tolerance of domestic broad-leaved evergreen tree species by low-temperature treatment. *J. Korean Soc. For. Sci.* **2019**, *108*, 484–492. (In Korean) [[CrossRef](#)]
53. Ren, Q.; Wang, R.P.; Sheng, X.Y.; Zhang, L. Modeling the potential distribution of *Machilus thunbergii* under the climate change patterns in China. *J. Geosci. Environ. Prot.* **2020**, *8*, 185–198. [[CrossRef](#)]
54. Nakao, K.; Higa, M.; Tsuyama, I.; Lin, C.-T.; Sun, S.-T.; Lin, J.-R.; Chiou, C.-R.; Chen, T.-Y.; Matsui, T.; Tanaka, N. Changes in the potential habitats of 10 dominant evergreen broad-leaved tree species in the Taiwan-Japan archipelago. *Plant Ecol.* **2014**, *215*, 639–650. [[CrossRef](#)]
55. Tang, C.Q.; Matsui, T.; Ohashi, H.; Nualart, N.; Herrando-Moraira, S.; Dong, Y.-F.; Grote, P.J.; Nguyen, V.N.; Hoang, V.S.; Li, S.; et al. Identifying long-term stable refugia for dominant *Castanopsis* species of evergreen broad-leaved forests in East Asia: A tool for ensuring their conservation. *Biol. Conserv.* **2022**, *273*, 109663. [[CrossRef](#)]
56. Cheuk, M.L.; Fischer, G.A. The impact of climate change on the distribution of *Castanopsis* (Fagaceae) species in South China and Indo-China region. *Glob. Ecol. Conserv.* **2021**, *26*, e01388. [[CrossRef](#)]
57. Kollmann, J.; Schill, H.-P. Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. *Vegetatio* **1996**, *125*, 193–205. [[CrossRef](#)]
58. Pons, J.; Pausas, J.G. Acorn dispersal estimated by radio-tracking. *Oecologia* **2007**, *153*, 903–911. [[CrossRef](#)] [[PubMed](#)]
59. Kominami, Y.; Sato, T.; Takeshita, K.; Manabe, T.; Endo, A.; Noma, N. Classification of bird-dispersed plants by fruiting phenology, fruit size and growth form in a primary lucidophyllous forest: An analysis, with implications for the conservation of fruit-bird interactions. *Ornithol. Sci.* **2003**, *2*, 3–23. [[CrossRef](#)]
60. Li, N.; Wang, Z.; Zhang, S.; Yan, C.; Li, X.; Lu, C. Importance of bird traits for seed dispersal patterns of co-fruited trees in a patchy forest. *Integr. Zool.* **2019**, *14*, 470–478. [[CrossRef](#)] [[PubMed](#)]
61. Bobiec, A.; Reif, A.; Öllerer, K. Seeing the oakscapes beyond the forest: A landscape approach to the oak regeneration in Europe. *Landsc. Ecol.* **2018**, *33*, 513–528. [[CrossRef](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.