



# 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

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## ARTICLE INFO

**Received** August 16, 2022

**Revised** November 15, 2022

**Accepted** November 16, 2022

**Published on** December 15, 2022

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**Background:** Climate change significantly influences the geographical distribution of plant species worldwide. Selecting indicator species allows for better-informed and more effective ecosystem management in response to climate change. The Korean Peninsula is the northernmost distribution zone of warm temperate evergreen broad-leaved (WTEB) species in Northeast Asia. Considering the ecological value of these species, we evaluated the current distribution range and future suitable habitat for 13 WTEB tree species designated as climate-sensitive biological indicator species.

**Results:** Up-to-date and accurate WTEB species distribution maps were constructed using herbarium specimens and citizen science data from the Korea Biodiversity Observation Network. Current northern limits for several species have shifted to higher latitudes compared to previous records. For example, the northern latitude limit for *Stauntonia hexaphylla* is higher (37° 02' N, Deokjeokdo archipelago) than that reported previously (36° 13' N). The minimum temperature of the coldest month (Bio6) is the major factor influencing species distribution. Under future climate change scenarios, suitable habitats are predicted to expand toward higher latitudes inland and along the western coastal areas.

**Conclusions:** Our results support the suitability of WTEB trees as significant biological indicators of species' responses to warming. The findings also suggest the need for consistent monitoring of species distribution shifts. This study provides an important baseline dataset for future monitoring and management of indicator species' responses to changing climate conditions in South Korea.

**Keywords:** climate change, habitat suitability, Korean Biodiversity Observation Network, northward shift, species distribution model

## Introduction

Over the past 40 years (1980–2019), the annual temperature in South Korea has increased by 1.4°C, exceeding the global average (Moon et al. 2020), and is projected to increase by 0.63°C per decade throughout the 21st century (National Institute of Meteorological Sciences 2019). Climate change has already impacted the species distribution and community structure in forest ecosystems of South Korea, as shown by poleward shifts in the geographic distribution of evergreen broad-leaved trees and reductions in the area of subalpine coniferous forest (Kim et al. 2019;

Yun et al. 2011a). If the average temperature rises by 1°C over the next 100 years in South Korea, the climate zone will move approximately 150 km northward and 150 m upward (Kong 2007). Thus, assessments of the impact of climate change on species distribution are necessary to reveal the extent of potential ecological risks.

Large-scale and long-term data are required to identify ecological changes in response to warming and enable better-informed and more effective ecosystem management for climate change mitigation and adaptation (Ims and Yoccoz 2017; Shin et al. 2021a; Urban et al. 2016). In particular, indicator species are important for monitoring envi-



ronmental changes, providing warnings of impending ecological shifts, and assessing the efficacy of ecosystem management decisions (Lee et al. 2010; Siddig et al. 2016). The National Institute of Biological Resources of South Korea has designated 130 climate-sensitive biological indicator species (CBIS), including vertebrate, invertebrate, and flora species, in order to monitor the influence of climate change on the distribution of biological species on the Korean Peninsula (National Institute of Biological Resources 2017). These CBIS are continuously monitored and managed to determine all changes in life cycle, distribution, or population size owing to climate change. Notably, the CBIS are intensively monitored through the Korean Biodiversity Observation Network (K-BON), which is a citizen science project in which citizens observe and record the surrounding biodiversity.

The climate of the Korean Peninsula includes both warm temperate and cold climate zones (Yun et al. 2020) and affects the geographical distribution limits of evergreen broad-leaved tree species in warm-temperature zones (Choi 2013; Eom and Kim 2020). South Korea is the northernmost distribution zone of warm temperate evergreen broad-leaved (WTEB) forests in Northeast Asia; thus, the distribution limits of WTEB trees in this region have important ecological value (Choi 2013; Eom and Kim 2020; Yun et al. 2011a). For example, the following northernmost distributions of evergreen broad-leaved tree species and their typical communities have been designated as natural monuments for conservation and research purposes (Cultural Heritage Administration 2003): the *Camellia japonica* population on Daechongdo Island, Ongjin (no. 66); the *Daphniphyllum macropodum* population on Naejangsan Mountain (no. 91); the *Neolitsea sericea* population at Bulgapsa temple, Yeonggwang (no. 112); the *Machilus thunbergii* population in Gyeokpo-ri, Buan (no. 123); the *Ilex crenata* population in Junggye-ri, Buan (no. 124); and the *Hedera rhombea* population of Samin-ri, Gochang (no. 367). Rising temperatures are likely to induce changes in the limited geographical distribution of WTEB trees in the warm temperate environments of South Korea. Already, the distribution of 57 broad-leaved evergreen tree species such as *Elaeagnus macrophylla* and *M. thunbergii* has shifted by more than 14–74 km to higher latitudes over the past 60 years (Yun et al. 2011a). Several other species have been reported at higher latitudes than their previously recorded northern limits (Kim et al. 2011; Lee and Choi 2010). However, the current distribution for each species does not include up-to-date records from recent flora surveys.

Quantifying the current distributional ranges of species is crucial for identifying shifts in response to future climate warming (Shin et al. 2021b). The impact of climate change on species can also be predicted using species distribution models, which are based on the statistical relationship between species occurrences and environmental

characteristics (Franklin 2013; Pearson and Dawson 2003). Thirteen species of WTEB trees have been designated as CBIS and are being intensively monitored nationwide (National Institute of Biological Resources 2019). Today, the increasing spatial and temporal extents of monitoring data for CBIS (National Institute of Biological Resources 2020) are expected to enhance our understanding of the distribution range of these 13 WTEB tree species. Therefore, the aim of this study was to determine the current distribution range and predict the future suitable habitat of 13 WTEB tree species designated as CBIS in South Korea. The specific objectives of this study were as follows: 1) to construct a dataset of species distribution based on accurate data; 2) to identify northern distribution limits based on the current distribution map; 3) to identify the major climatic variables affecting species distribution; 4) to predict the suitable habitat ranges under current and future climate conditions. Our results provide useful baseline data for future monitoring and management of CBIS responses to changing climate conditions.

## Materials and Methods

### Study site and species

South Korea (33°–38° N, 124°–131° E) is located within the middle latitudes of the Northern Hemisphere, on the east coast of the Eurasian Continent and adjacent to the Western Pacific (National Geographic Information Institute 2020). It has a temperate climate with four seasons and substantial precipitation in comparison with that of the Eurasian continental features. Subalpine coniferous, deciduous broad-leaved, and warm temperate evergreen forests are common in the northern, central, and southern and island regions, respectively.

We selected the following 13 WTEB tree species designated as CBIS in South Korea: *Ardisia japonica* (Thunb.) Blume; *Aucuba japonica* Thunb.; *Camellia japonica* L.; *Daphniphyllum macropodum* Miq.; *Elaeagnus macrophylla* Thunb.; *Eurya japonica* Thunb.; *Hedera rhombea* (Miq.) Bean; *Ilex crenata* Thunb.; *Machilus thunbergii* Siebold & Zucc.; *Neolitsea sericea* (Blume) Koidz.; *Pittosporum tobira* (Thunb.) W. T. Aiton; *Rhaphiolepis indica* var. *umbellata* (Thunb.) Ohashi; and *Stauntonia hexaphylla* Decne. (National Institute of Biological Resources 2019). These species are mainly distributed along islands and/or coasts in the southern and western provinces of South Korea, and are predicted to experience a poleward shift in response to future warming.

### Data collection and validation

We collected distribution records for the 13 WTEB tree species from specimens deposited at the herbarium of the National Institute of Biological Resources in South Korea

(KB) (<https://species.nibr.go.kr/>) and the K-BON citizen science dataset. Civic organizations and citizen scientists in the K-BON observe the surrounding biodiversity and record their information (i.e., date, species name, geological location, and photos) using the citizen science platform NATURING (<http://www.naturing.net/>).

To determine the accuracy of the collected distribution data, we performed a validation process for all records. In the case of herbarium specimens, we included only records with the collection ID 'NIBRVP-', indicating that they had been confirmed by internal experts. We discarded records with obvious geocoding errors such as mismatches between administrative districts and coordinates, as well as those located in the ocean. For the citizen science data in K-BON, we selected only records with geotagged photographs in the NATURING platform. We then followed the validation procedure of species identification by experts to ensure the accuracy of the citizen science data. Finally, planted records located in villages, botanical gardens, and parks were deleted from the dataset.

We then constructed a database of valid species distributions for 13 WTEB tree species consisting of administrative districts, coordinates, date, and references (Tables S1–S13). All records were mapped according to the WGS84 coordinate system using the ArcMAP 10.0 geographical information software package (ESRI, Redlands, CA, USA). We also established the northern distribution limit by connecting the northernmost latitude points for the West Sea–Inland–East Sea on the species distribution map.

## Environmental variables and climate change scenarios

We downloaded 19 bioclimatic factors related to temperature and precipitation changes with a resolution of 30 arc-seconds from the WorldClim database v. 2.1 (<http://www.worldclim.org/>), which provides average data for 1970–2000. These variables represent annual trends (e.g., mean annual temperature and precipitation), seasonality (annual range of temperature and precipitation), and extreme or limiting environmental factors (temperature of the coldest and warmest month; precipitation in wet and dry quarters) (Fick and Hijmans 2017). Many of the bioclimatic variables were spatially correlated, which can result in model over-fitting when simulating the potential species distribution (Cook and Ranstam 2016). To reduce multi-collinearity among these variables, highly correlated variables (Pearson's correlation coefficients  $|r| > 0.70$ ) were excluded from the modeling process. We also considered previous studies (Koo et al. 2001; Yun et al. 2011b) that highlighted winter temperature as an important climate element contributing to the distribution limits of evergreen broad-leaved trees. Finally, six bioclimatic variables (Bio3, 5, 6, 12, 13, and 19) were selected for establishing the model (Table 1). Future climate data were obtained from the

**Table 1** Bioclimatic variables used to predict the potential distribution of 13 warm temperate evergreen broad-leaved tree species designated as climate-sensitive biological indicator species in South Korea

Variable code	Description (Unit)
Bio3	Isothermality ((Bio2/Bio7) × 100 (%))
Bio5	Maximum temperature of warmest month (°C)
Bio6	Minimum temperature of coldest month (°C)
Bio12	Annual precipitation (mm)
Bio13	Precipitation of wettest month (mm)
Bio19	Precipitation of coldest quarter (mm)

Bio2: the mean of the monthly temperature ranges (monthly maximum – monthly minimum); Bio7: temperature annual range.

Hadley Centre Global Environmental Model in the Global Coupled configuration 3.1 (HadGEM3-GC3.1), which was submitted to the sixth Coupled Model Intercomparison Project by the United Kingdom (Williams et al. 2017). The climate models developed by the Met Office Hadley Centre of the United Kingdom have been used in climate change studies in many countries, including Korea. In particular, the recently released HadGEM3-GC3.1 has been improved for many variables including greenhouse gases, aerosols, solar irradiance, volcanic aerosols, land use, and ozone concentrations (Andrews et al. 2020). We performed the future climate projections with the same spatial resolution as the current data for the 2070s (average for 2061–2080) under the two Shared Socioeconomic Pathway (SSP) scenarios (i.e., SSP2-4.5 and SSP5-8.5). SSPs provide different levels of socioeconomic challenges that will alter the degree of achievable climate change mitigation and adaptation (O'Neill et al. 2014). SSP2-4.5 represents a moderate challenge to mitigation and adaptation and combines intermediate societal vulnerability with an intermediate forcing level. SSP5-8.5 is characterized by high socioeconomic challenges to mitigation and low socioeconomic challenges to adaptation.

## Species distribution modeling

Species distribution models were created using Maximum Entropy software v. 3.4.1 ([http://biodiversityinformatics.amnh.org/open\\_source/maxent/](http://biodiversityinformatics.amnh.org/open_source/maxent/)). This is one of the most popular tools based on presence-only occurrence records for modeling that has high predictive power across all sample sizes; thus, it is widely used to predict the distribution of many taxa (Elith et al. 2011; Kaky et al. 2020). To minimize the sampling bias effect in the datasets, we randomly selected only one record per grid cell (30 arc-seconds, consistent with the resolution of bioclimatic data) using ArcToolBox in Arc GIS 10.4.1 (ESRI). We mostly used the default settings in MaxEnt (i.e., linear, quadratic, and hinge features) (Phillips et al. 2006), except for the following settings: 30% random test percentage, 10-fold cross-validation, logistic output format and threshold rules

with the maximum training sensitivity plus specificity. Model performance was evaluated using the area under the curve (AUC) values of the receiver operating characteristics curves. AUC values below 0.7 were considered poor, values between 0.7 and 0.8 were considered fair, values between 0.8 and 0.9 were considered good, and those above 0.9 were considered excellent (Phillips et al. 2006). For a better interpretation of species distribution changes under current and future climate conditions, we converted the potential distribution projections into binary maps (suitable and unsuitable habitats) according to the threshold value.

## Results

### Current distribution range and northern limit

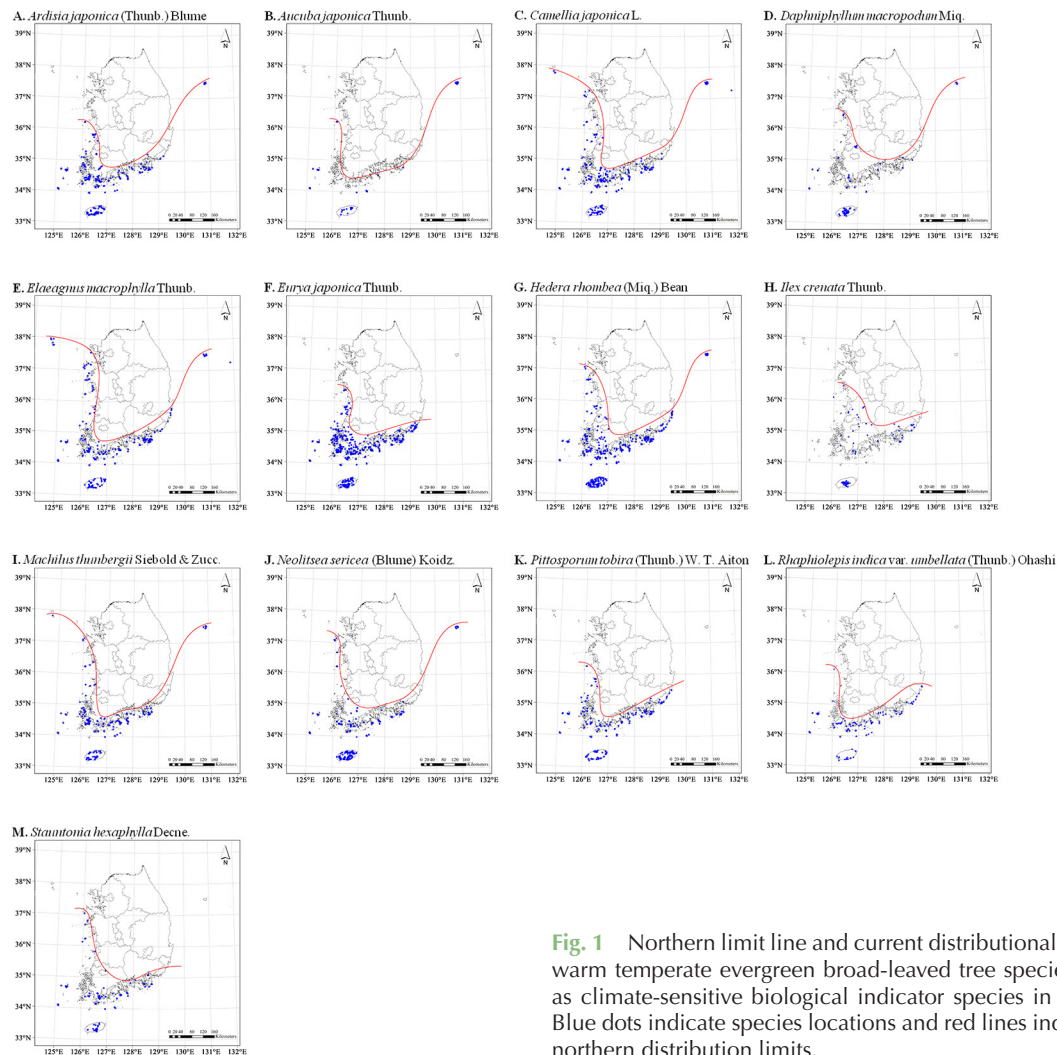
In this study, we constructed a distribution dataset for 13 WTEB tree species designated as CBIS using specimens and K-BON data (Tables S1–S13). More than 100 distribution records were collected for all species except *Au. japonica* (77 records). For *E. japonica*, a total of 603 records were collected from specimens (496) and K-BON data (107). The

northern limit lines were identified by connecting the northernmost points on the species distribution map (Table 2, Fig. 1). In the west, the island regions on Ongjin-gun (37° 02'–37° 58' N in latitude) of Incheon metropolitan city were identified as the northern limit region of six species, including *C. japonica*, *E. macrophylla*, *H. rhombea*, *M. thunbergii*, *N. sericea*, and *S. hexaphylla*. At lower latitudes, Taean-gun (36° 29' N) of Chungcheongnam-do was confirmed as the northern limit region of *D. macropodium* and *I. crenata*, and Boryeong-si (36° 13'–36° 22' N) represented the northern limit for four species (i.e., *Ar. japonica*, *Au. japonica*, *E. japonica*, and *P. tobira*). The northern limit region of *R. indica* var. *umbellata* was Gunsan-si (36° 07' N) of Jeollabuk-do, which had the lowest latitude of all northern limits identified in this study. In the east, Ulleung-gun (37° 30'–37° 32' N) of Gyeongsangbuk-do was identified as the northern limit region of eight species, including *Ar. japonica*, *Au. japonica*, *C. japonica*, *D. macropodium*, *E. macrophylla*, *H. rhombea*, *M. thunbergii*, and *N. sericea*. The northern limit regions confirmed for other species at lower latitudes included Ulsan metropolitan city (35° 29'–35° 36' N) for *P. tobira* and *R. indica* var. *umbella-*

**Table 2** Latitudes of the northern distribution limit of 13 warm temperate evergreen broad-leaved tree species designated as climate-sensitive biological indicator species in South Korea

No.	Scientific name	Latitudes of the northern distribution limit				
		Uyeki (1941)	Yun et al. (2011a)	Our study		No. of records
			West	East		
1	<i>Ardisia japonica</i> (Thunb.) Blume	36° 10'	36° 07'	36° 13' (Oeyeondo, Boryeong-si)	37° 30' (Ulleung-gun)	344
2	<i>Aucuba japonica</i> Thunb.	37° 50'	35° 37'	36° 14' (Oeyeondo, Boryeong-si)	37° 31' (Ulleung-gun)	77
3	<i>Camellia japonica</i> L.	-	-	37° 50' (Daecheongdo, Ongjin-gun)	37° 31' (Ulleung-gun)	347
4	<i>Daphniphyllum macropodium</i> Miq.	35° 37'	36° 28'	36° 29' (Taean-gun)	37° 31' (Ulleung-gun)	116
5	<i>Elaeagnus macrophylla</i> Thunb.	36° 10'	37° 56'	37° 58' (Baengnyeongdo, Ongjin-gun)	37° 31' (Ulleung-gun)	287
6	<i>Eurya japonica</i> Thunb.	36° 10'	36° 24'	36° 22' (Wonsando, Boryeong-si)	35° 19' (Busan)	603
7	<i>Hedera rhombea</i> (Miq.) Bean	36° 10'	37° 01'	37° 05' (Baekado, Ongjin-gun)	37° 31' (Ulleung-gun)	495
8	<i>Ilex crenata</i> Thunb.	-	-	36° 29' (Taean-gun)	35° 16' (Busan)	115
9	<i>Machilus thunbergii</i> Siebold & Zucc.	36° 10'	37° 03'	37° 50' (Daecheongdo, Ongjin-gun)	37° 32' (Ulleung-gun)	265
10	<i>Neolitsea sericea</i> (Blume) Koidz.	35° 12'	37° 03'	37° 07' (Gakheuldo, Ongjin-gun)	37° 31' (Ulleung-gun)	307
11	<i>Pittosporum tobira</i> (Thunb.) W. T. Aiton	36° 10'	36° 13'	36° 13' (Oeyeondo, Boryeong-si)	35° 29' (Ulsan)	203
12	<i>Rhaphiolepis indica</i> var. <i>umbellata</i> (Thunb.) Ohashi	35° 15'	35° 09'	36° 07' (Eocheongdo, Gunsan-si)	35° 36' (Ulsan)	169
13	<i>Stauntonia hexaphylla</i> Decne.	36° 10'	36° 13'	37° 02' (Deokjeokdo, Ongjin-gun)	35° 05' (Changwon-si)	123

Administrative districts are shown in parentheses.



**Fig. 1** Northern limit line and current distributional ranges for 13 warm temperate evergreen broad-leaved tree species designated as climate-sensitive biological indicator species in South Korea. Blue dots indicate species locations and red lines indicate species northern distribution limits.

ta, Busan metropolitan city (35° 16'–35° 19' N) for *E. japonica* and *I. crenata*, and Changwon-si (35° 05' N) of Gyeong-sangnam-do for *S. hexaphylla*.

### Climatic variables affecting species spatial distribution

The distribution models for 13 WTBE tree species had AUC values > 0.90, indicating excellent model fit to the data (Table 3). The major bioclimatic variables affecting the spatial distribution differed among species. The distribution of *Au. japonica* was mainly affected by precipitation of the coldest quarter (Bio19, contribution 50.1%) and isothermality (Bio3, 23.8%). For *D. macropodum*, annual precipitation (Bio12, 44.4%), Bio19 (21.2%), and Bio3 (20.4%) were the major variables impacting habitat suitability. Bio12 (57.5%) and the minimum temperature of the coldest month (Bio6, 34.7%) were identified as the major factors for *I. crenata*. For 10 species, including *Ar. japonica*, *C. japonica*, *E. macrophylla*, *E. japonica*, *H. rhombea*, *M. thunbergii*, *N. sericea*, *P. tobira*, *R. indica* var. *umbellata*, and *S. hexaphylla*, Bio6 was identified as the main variable affecting species distribution.

The response curves of the major bioclimatic variables showed the most likely ranges of occurrence for the 13 WTBE tree species (Fig. 2). According to the response curves for the two largest contributing climatic variables, the occurrence probability of *Au. japonica* increased when Bio19 was greater than approximately 180 mm and Bio3 was less than approximately 24% (probability of presence > 0.5). *Daphniphyllum macropodum* preferred habitats with Bio12 > 1,700 mm and Bio19 > 170 mm. The optimal Bio12 for *I. crenata* occurrence was > 1,650 mm, with Bio6 ranging from –4.0°C to 1.0°C. Bio6 was the best predictor of the distribution of 10 WTBE tree species and had the following optimal ranges: > –4.0°C for *Ar. japonica*; –2.0 to 3.0°C for *C. japonica*; > –2.0°C for *E. macrophylla*; –2.5 to 2.5°C for *E. japonica*; > –2.0°C for *H. rhombea*; > –2.0°C for *M. thunbergii*; > –1.5°C for *N. sericea*; > –0.5°C for *P. tobira*; > –1.0°C for *R. indica* var. *umbellata*; and –1.5 to 3.0°C for *S. hexaphylla*.

### Predicted potential distribution under current and future climate conditions

Current suitable habitats for 13 WTBE tree species were

**Table 3** Sample size, model performance, and contribution of major bioclimatic variables for the species distribution models of 13 warm temperate evergreen broad-leaved tree species designated as climate-sensitive biological indicator species in South Korea

No.	Scientific name	Occurrence data	AUC	Major bioclimatic variables (contribution %)		
1	<i>Ardisia japonica</i> (Thunb.) Blume	178	0.969	Bio6 (72.9)	Bio3 (14.9)	Bio19 (6.9)
2	<i>Aucuba japonica</i> Thunb.	43	0.992	Bio19 (50.1)	Bio3 (23.8)	Bio6 (17.3)
3	<i>Camellia japonica</i> L.	169	0.967	Bio6 (82.5)	Bio5 (10.0)	Bio3 (4.5)
4	<i>Daphniphyllum macropodum</i> Miq.	68	0.967	Bio12 (44.4)	Bio19 (21.2)	Bio3 (20.4)
5	<i>Elaeagnus macrophylla</i> Thunb.	137	0.965	Bio6 (70.4)	Bio3 (17.2)	Bio5 (6.3)
6	<i>Eurya japonica</i> Thunb.	323	0.951	Bio6 (83.0)	Bio3 (10.4)	Bio19 (3.6)
7	<i>Hedera rhombea</i> (Miq.) Bean	246	0.955	Bio6 (84.2)	Bio3 (5.9)	Bio5 (5.7)
8	<i>Ilex crenata</i> Thunb.	73	0.915	Bio12 (57.5)	Bio6 (34.7)	Bio19 (6.6)
9	<i>Machilus thunbergii</i> Siebold & Zucc.	127	0.969	Bio6 (75.8)	Bio3 (17.2)	Bio5 (2.6)
10	<i>Neolitsea sericea</i> (Blume) Koidz.	151	0.973	Bio6 (67.6)	Bio3 (11.8)	Bio5 (9.3)
11	<i>Pittosporum tobira</i> (Thunb.) W.T. Aiton	81	0.978	Bio6 (87.5)	Bio5 (4.3)	Bio19 (3.2)
12	<i>Raphiolepis indica</i> var. <i>umbellata</i> (Thunb.) Ohashi	61	0.983	Bio6 (81.2)	Bio3 (8.4)	Bio19 (7.2)
13	<i>Stauntonia hexaphylla</i> Decne.	67	0.977	Bio6 (72.3)	Bio3 (15.2)	Bio19 (6.4)

AUC: area under the curve; Bio3: isothermality; Bio5: maximum temperature of warmest month; Bio6: minimum temperature of coldest month; Bio12: annual precipitation; Bio13: precipitation of wettest month; Bio19: precipitation of coldest quarter.

predicted in coastal areas of western and southern provinces in South Korea, where these species currently exist (Fig. 3). We also predicted potential suitable habitats in the Yeongdong coastal region of Gangwon-do, where these species are currently absent. Future projections to the 2070s showed that the distribution of WTEB tree species may extend to inland areas, which are at a higher latitude than that of current habitats (Fig. 3). Under the future climate scenario of SSP2-4.5, a suitable habitat was predicted along the western coastal areas of the metropolitan region and Chungcheongnam-do. Expansion toward higher latitudes was more marked under SSP5-8.5 than under SSP2-4.5. *Ilex crenata* was predicted to occupy all regions except several mountainous regions of Gangwon-do (Fig. 3H). Conversely, the potential habitat of *Au. japonica* was predicted to occupy a narrower range than other species under future climate scenarios.

## Discussion

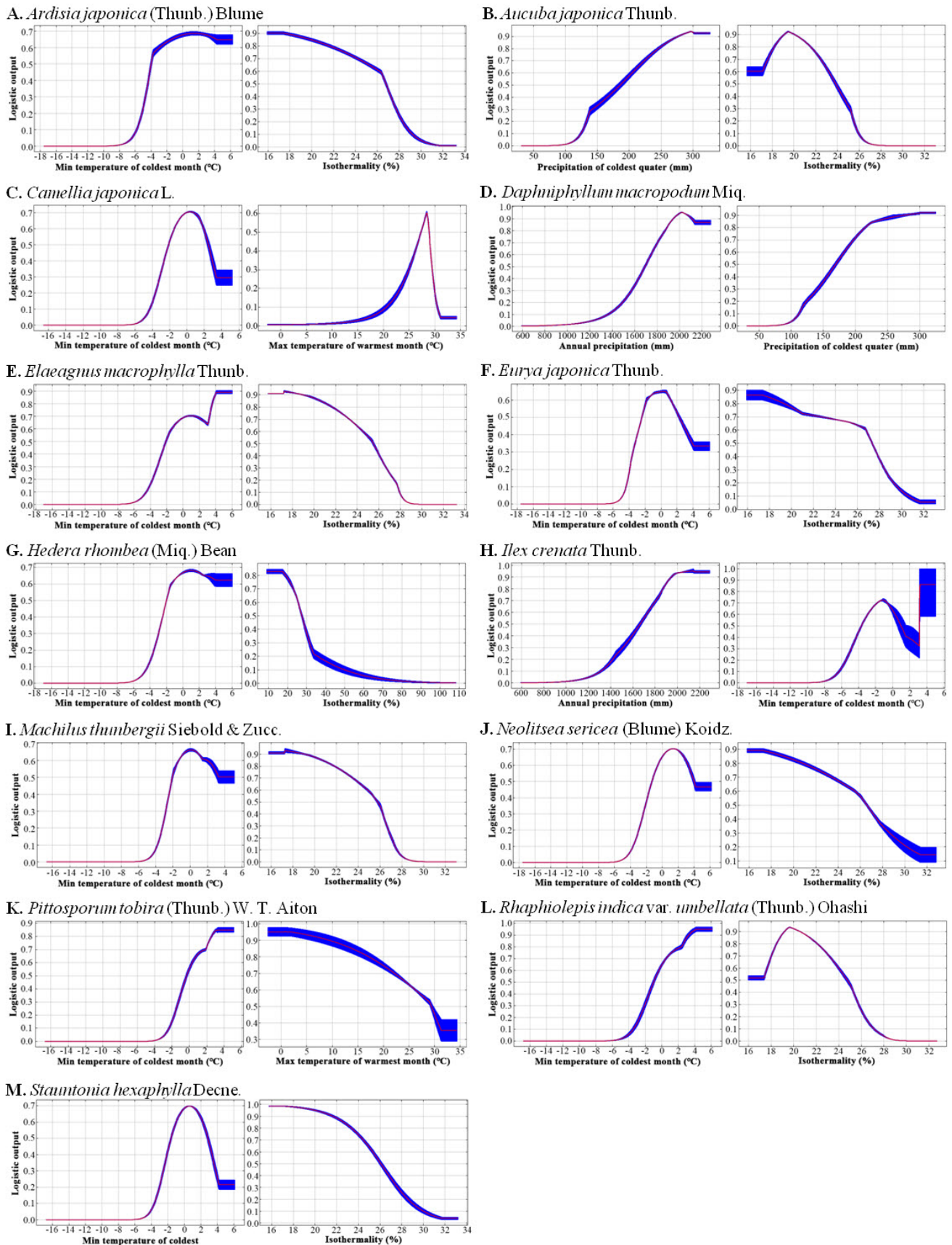
### Current distribution range and northern limits as baseline data for monitoring

Climate change significantly influences the geographical distributions of plant species worldwide (Kelly and Goulden 2008; Liang et al. 2018). Previous studies have reported the distribution and northern limits of WTEB tree species in relation to increased temperatures in South Korea. For example, Uyeki (1941) described the northern limit of 64 WTEB tree species on Daecheongdo Island–Byeonsan–Yeongam–Jukdo Island–Ulleungdo Island. Since then, Yun et al. (2011a) reported a northward shift of WTEB tree species from their previous limit to Baengnyeongdo Island–Cheongyang–Jeongeup–Pohang–Ulleungdo Island. Here, we constructed current distribution ranges to identify

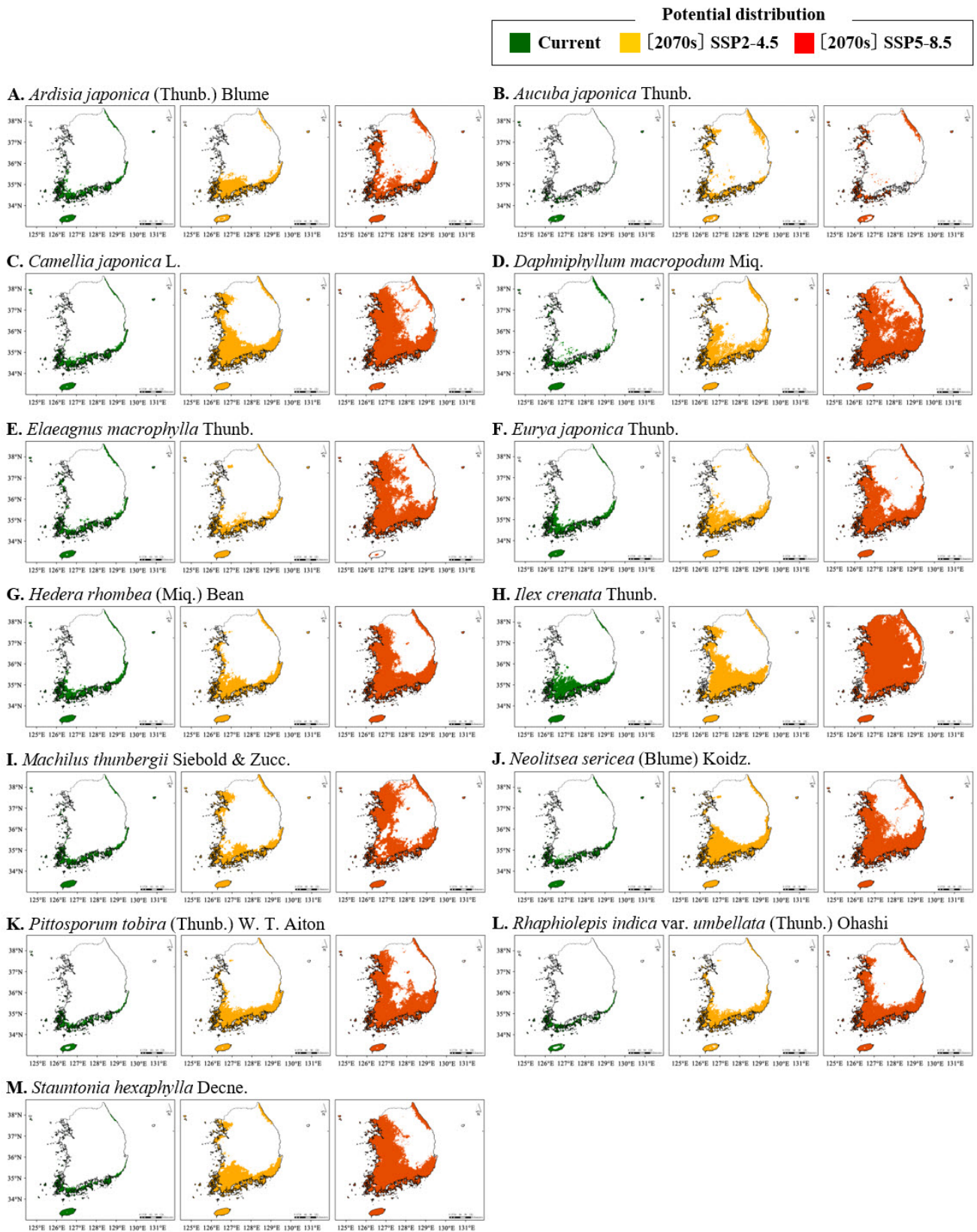
up-to-date northern limits for 13 WTEB tree species designated as CBIS from a total of 3,451 herbarium specimens and K-BON data.

In our study, the northern limits for several species were identified at higher latitudes than previous records (Table 2). The distribution of *Ar. japonica* shifted upward from 36° 07' N (Yun et al. 2011a) to 36° 13' N (Oeyeondo Island). The northern limit of *Au. japonica* shifted from 35° 37' N (Yun et al. 2011a) to 36° 14' N (i.e. Oeyeondo Island) in the west and to 37° 31' N (Ulleungdo Island) in the east. Yun et al. (2011a) reported lower latitudes for the northern limits of *Au. japonica* than Uyeki (1941) (37° 50' N), which was attributed to species misidentification and/or habitat destruction at high latitudes. Our data showed higher latitudes than Yun et al. (2011a) and slightly lower latitudes than Uyeki (1941) for the northern limits of *Au. japonica*. For *M. thunbergii* and *N. sericea*, our data showed a new distribution at 37° 07' N (Gakheuldo Island), with higher latitudes than previously recorded (37° 03' N; Yun et al. 2011a). However, some studies have reported a higher latitude distribution of *M. thunbergii* (Daecheongdo Island, 37° 50' N) than that determined in this study (Lee and Choi 2010; Yang et al. 2012; Son et al. 2016). Thus, we established Daecheongdo Island as the northern limit of *M. thunbergii* to account for recent research. The northern limit of *R. indica* var. *umbellata* shifted upward from 35° 09' N (Yun et al. 2011a) to 36° 07' N (Eocheongdo Island). For *S. hexaphylla*, the distribution record newly collected from the Deokjeokdo archipelago of Incheon metropolitan city using citizen data from K-BON revealed an upward shift in the northern limit from 36° 13' N (Yun et al. 2011a) to 37° 02' N. Citizen data were also an important source for understanding the distribution ranges of other WTEB tree species in this study.

The West Sea Islands lie at the northernmost line in the



**Fig. 2** Response curves for the two largest contributing variables for 13 warm temperate evergreen broad-leaved tree species designated as climate-sensitive biological indicator species under current climate conditions. The response curves indicate the correlation between climatic variables and the probability of species presence.



**Fig. 3** Predicted changes in the suitable habitat of 13 warm temperate evergreen broad-leaved tree species designated as climate-sensitive biological indicator species under current and future climate conditions. Future predictions are based on climate change scenarios SSP2-4.5 and SSP5-8.5 for the 2070s (average for 2061–2080).

west of the southern coast floristic subregion of South Korea and are a very important region in terms of plant geography as they define the northern limits of many warm

temperate broad-leaved species (Lee and Choi 2008; Kim et al. 2011). The West Sea Islands also allow the northward distribution of many southern plants under the influence

of the West Sea Warm Current; however, accurate species distributions are unknown because of a lack of sufficient research on this island area. More recently, a new distribution of plant species has been reported on the islands through floristic studies of uninhabited islands and a detailed survey of specific islands; this was prompted by the need to understand the flora of the island region and the ease of survey access (Lee and Choi 2008, 2010; Kim et al. 2011; Son et al. 2016; Song et al. 2021). In our study, the northern limits for several species were identified at higher latitudes than previously recorded (Yun et al. 2011a). However, it is unclear if this northward species distribution shift is due to climate change, as we do not know whether they were distributed this way in the past but were just now discovered, or whether this is a novel distribution resulting from climate change. Nevertheless, establishing the current northern limits in our study provide key baseline data for detecting future shifts in species distribution. In particular, subsequent continuous monitoring data can reveal the geographical responses of species to climate changes.

The latitudes of the northern distribution limits for *C. japonica* and *I. crenata* were not addressed by Yun et al. (2011a) because these trees are planted in urban areas, outside of their natural distribution range. In this study, we identified 37° 50' N (Daecheongdo Island) and 36° 29' N (Tae-an-gun) as the northern limits for *C. japonica* and *I. crenata*, respectively, using only records from their natural habitat. Aside from these two species, many evergreen broad-leaved trees are being planted in parks, villages, and streets for landscape purposes, with *D. macropodum*, *P. tobira*, and *R. indica* var. *umbellata* particularly favored as landscape species (Park et al. 2015b). Climate change has allowed warm temperate species that typically occupy warm environments along southern and western coastal areas to be planted further inland and at higher latitudes. Indeed, seed dispersal from planted individuals may lead to species becoming established on new sites. Therefore, planting-related distribution changes should also be considered when determining the impact of climate change on species distributions.

### Factors influencing habitat suitability

Climate is a key factor impacting species distribution. In particular, identifying the climatic conditions of the northernmost regions of warm temperate forests is an important research topic for classifying vegetation zones and monitoring vegetation community structure. Many studies have reported the climatic conditions that characterize the distribution of warm temperate trees (Koo et al. 2001; Yun et al. 2011b; Eum and Kim 2020). Eum and Kim (2020) reported that the annual mean temperature of the northern limits of the warm temperate forest zone was 13–14°C (Eum and Kim 2020). Koo et al. (2001) highlighted the winter temperature as an important climate element con-

tributing to the distribution limits of WTEB plants, with a mean temperature of  $-4^{\circ}\text{C}$  and a mean minimum temperature of  $-9^{\circ}\text{C}$  in January. Yun et al. (2011b) also revealed that the minimum temperature of the coldest month, which determines the distribution of WTEB trees, was  $-5.95^{\circ}\text{C}$ . In this study, we found that the minimum temperature of the coldest month (Bio6) was a major factor contributing to the distribution of 10 WTEB tree species (Table 3) and was positively correlated with the habitat suitability of these species (Fig. 2). Although there was a slight difference in the temperature range that correlated with an increased occurrence probability for each species, most species preferred the minimum temperature of the coldest month to be at least  $-4.0^{\circ}\text{C}$ .

For *Au. japonica*, *D. macropodum*, and *I. crenata*, precipitation-related variables (Bio19 and Bio12) were the main factors affecting their spatial distribution rather than temperature (Fig. 2). Park et al. (2015a) identified the annual precipitation as the main factor affecting the distribution of *D. macropodum*, which typically grows in habitats with annual precipitation over 1,500 mm and high soil moisture. Our results also revealed that two precipitation-related variables (Bio12 and Bio19) explained 65.6% of the total variance, so they were confirmed as the main factors affecting the spatial distribution of this species. Specifically, the distribution probability of *D. macropodum* increased (>50%) in areas with an annual precipitation above 1,700 mm and precipitation in the coldest quarter (i.e., the winter season) of greater than 170 mm. In addition, the temperate-related variable isothermality (Bio3) explained 20.4% of the total variance so was identified as another important factor affecting the spatial distribution of *D. macropodum*.

In this study, the major factors affecting the distribution and preferred climate range of each species were identified by extracting the current climatic variables based on actual species locations. Our results were consistent with those of previous studies revealing the impact of winter temperature as a major factor on species distribution. Precipitation-related variables were also significant factors affecting several species' spatial distribution. These results provide an important basis for understanding changes in the distribution of indicator species under future climate conditions.

### Potential suitable habitat expansion under future climate conditions

According to the future projection of climate zones for the Korean Peninsula, the temperate climate zone in the southern region is predicted to gradually expand and occupy most of the Korean Peninsula by 2100 (Yun et al. 2020). Future climatic conditions may lead to expansion of the distribution range of warm temperate tree species that prefer warm environments, with the suitable habitats of

southern species already predicted to increase under future climate change (Yun et al. 2011b; Koo et al. 2018). Our study also revealed a potential expansion in the distribution range of 13 WTEB tree species during 2061–2080 under two climate change scenarios (Fig. 3). These expanded trends toward higher latitudes coincide with previous studies on *C. japonica* (Koo et al. 2018), *E. japonica* (Yun et al. 2017), *H. rhombea* (Park et al. 2016), *M. thunbergii* (Yu et al. 2020), and *N. sericea* (Yun et al. 2014; Koo et al. 2018; Yu et al. 2020). *Daphniphyllum macropodum* and *I. crenata* showed faster expansion within inland and coastal areas of higher latitudes, with a projected increase in future annual precipitation of approximately 13% from present. Conversely, the future suitable habitat of *Au. japonica* was predicted to be more limited than that of other species. This species exhibited a narrow distribution range on Jeju-do and several coastal areas and islands of the southern region in the current (Fig. 1B), which will likely limit its expansion to higher latitudes and inland in the future. We confirmed that the minimum temperature of the coldest month was the major factor contributing to the distribution of the other 10 species exhibiting future expansion of their suitable habitat (Table 3). The minimum temperature of the coldest month in South Korea currently ranges from  $-15.6^{\circ}\text{C}$  to  $4.3^{\circ}\text{C}$  (1990–2010), but is projected to steadily increase to  $-11.2^{\circ}\text{C}$  to  $8.9^{\circ}\text{C}$  in the future (i.e., 2070s). Thus, future increases in winter temperature will induce expansion of the suitable habitats of warm temperate tree species that prefer a warm environment.

Although increasing temperature and precipitation are projected to expand the distribution of warm temperate tree species, the actual distribution is affected by more complex factors, including biotic and terrain factors (Leach et al. 2016). For example, the warming-induced invasion of exotic species and habitat destruction from human activities can limit such distribution shifts. In particular, distributional shifts and/or migration of plant species were limited by the dispersal process (Koo et al. 2018). In our study, the potential habitats of WTEB species included the Yeongdong coastal region of Gangwon-do, which is far from their actual distribution. Because we only considered climatic factors when constructing the species distribution models, our results show the climatic habitat suitability of 13 WTEB species. Furthermore, considering the ecological characteristics of the target species when predicting their potential distribution will improve the accuracy of predictions related to the responses of the species to future environmental changes. Nevertheless, our species distribution model exhibited excellent performance, revealing the key role of temperature-related variables and predicting the expansion of suitable habitat areas under future global climate change.

## Conclusions

This study reveals the current distribution range and future suitable habitats of 13 WTEB tree species designated as CBIS in South Korea. The major contribution of this study was the construction of up-to-date and accurate distribution maps based on herbarium specimens collected from multiple flora surveys as well as real-time K-BON citizen science data collected nationwide. Our findings confirmed the important role of citizen science data in understanding the distribution ranges of CBIS. This study also revealed an upward shift in the northern limits of several species when compared to their previous distributional ranges, as well as the expansion of suitable habitats under future climate change scenarios. Our results support the suitability of these 13 WTEB tree species as significant biological indicators of species responses to warming, highlighting the need for the continuous monitoring of their population demographics and distribution shifts. The database developed in this study also provides useful baseline data for identifying future shifts in species responses to climate change in South Korea.

## Supplementary Information

Supplementary information accompanies this paper at <https://doi.org/10.5141/jee.22.053>.

**Table S1.** Distribution records of *Ardisia japonica* (Thunb.) Blume in South Korea collected from specimens and the Korea Biodiversity Observation Network. **Table S2.** Distribution records of *Aucuba japonica* Thunb. in South Korea collected from specimens and the Korea Biodiversity Observation Network. **Table S3.** Distribution records of *Camellia japonica* L. in South Korea collected from specimens and the Korea Biodiversity Observation Network. **Table S4.** Distribution records of *Daphniphyllum macropodum* Miq. in South Korea collected from specimens and the Korea Biodiversity Observation Network. **Table S5.** Distribution records of *Elaeagnus macrophylla* Thunb. in South Korea collected from specimens and the Korea Biodiversity Observation Network. **Table S6.** Distribution records of *Eurya japonica* Thunb. in South Korea collected from specimens and the Korea Biodiversity Observation Network. **Table S7.** Distribution records of *Hedera rhombea* (Miq.) Bean in South Korea collected from specimens and the Korea Biodiversity Observation Network. **Table S8.** Distribution records of *Ilex crenata* Thunb. in South Korea collected from specimens and the Korea Biodiversity Observation Network. **Table S9.** Distribution records of *Machilus thunbergii* Siebold & Zucc. in South Korea collected from specimens and the Korea Biodiversity Observation Network. **Table S10.** Distribution records of *Neolitsea sericea* (Blume) Koidz. in South Korea collected

from specimens and the Korea Biodiversity Observation Network. **Table S11.** Distribution records of *Pittosporum tobira* (Thunb.) W. T. Aiton in South Korea collected from specimens and the Korea Biodiversity Observation Network. **Table S12.** Distribution records of *Rhaphiolepis indica* var. *umbellata* (Thunb.) Ohashi in South Korea collected from specimens and the Korea Biodiversity Observation Network. **Table S13.** Distribution records of *Stauntonia hexaphylla* Decne. in South Korea collected from specimens and the Korea Biodiversity Observation Network.

### Abbreviations

AUC: Area under the curve

CBIS: Climate-sensitive biological indicator species

HadGEM3-GC3.1: Hadley Centre Global Environmental Model in the Global Coupled configuration 3.1

K-BON: Korea Biodiversity Observation Network

SSP: Shared Socioeconomic Pathway

WTEB: Warm temperature evergreen broad-leaved

### Acknowledgements

We are grateful to the many citizen scientists that participated in the K-BON project, whose monitoring and records allowed us to construct an up-to-date and accurate species distribution dataset. We also thank the anonymous reviewers for their helpful comments on drafts of this article.

### Authors' Contribution

SS conceived the ideas, conducted the data collection and analysis, and wrote the manuscript. JHK conceived the ideas, checked the database, and reviewed the manuscript. DK conducted the data collection and analysis. JSK and HDJ checked the database and reviewed the manuscript. HGK conceived the ideas and reviewed the manuscript. JL and JEH reviewed the manuscript. HKO examined the manuscript. All authors read and approved the final manuscript.

### Funding

This work was supported by a grant from the National Institute of Biological Resources (NIBR), funded by the Ministry of Environment (MOE) of the Republic of Korea (NIBR202225101).

### Availability of data and materials

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

### Ethics approval and consent to participate

Not applicable.

### Consent for publication

Not applicable.

### Competing interest

The authors declare that they have no competing interests.

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