



Projected future distributions of dominant tree species in the Western Black Sea region under climate change scenarios

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Abstract

Habitat suitability models are widely used to estimate the potential distribution of species under current and future environmental conditions. In this study, the IPSL-CM6A-LR model and climate scenarios from the CMIP6 were employed to simulate future climate conditions. Using MaxEnt modeling, the future distributions of five dominant tree species (*Pinus nigra*, *Abies nordmanniana*, *Fagus orientalis*, *Quercus* spp., and *Pinus sylvestris*) in the Western Black Sea region were projected for the years 2030, 2050, 2070, and 2090 under the Shared Socioeconomic Pathways SSP 2-4.5 and SSP 5-8.5. Results under the SSP 2-4.5 scenario indicated a general loss of suitable habitats for all species, with *Quercus* spp. showing the highest reduction (6.1%), whereas very suitable zones increased for most species except *Pinus nigra*, which declined by 4.3%. Under the SSP 5-8.5 scenario, only *Abies nordmanniana* exhibited an increase (5%) in suitable habitat, while other species experienced contractions, resulting in a net loss of 12.3%; nevertheless, very suitable areas increased overall by 7.3%. In addition, this study assessed both current and future potential species mixtures by identifying stand-type combinations derived from overlapping suitable habitats. While *Fagus orientalis* and *Quercus* spp. currently dominate mixed stands, future projections suggest increasing overlap between *Abies nordmanniana* and *Pinus sylvestris*, particularly under SSP 5-8.5. Overall, species exhibited distinct and contrasting responses to future climate conditions across both scenarios. Variable importance analyses revealed that temperature seasonality, precipitation of the driest month, and isothermality were the primary environmental drivers shaping the current and future distributions of the studied tree species. Such analysis of dynamic species associations has not been previously addressed in the literature at this scale. By integrating spatial species distribution modeling with forest stand-type composition analysis, this study provides novel insights into how climate change may reshape forest structure and biodiversity, offering critical guidance for adaptive forest planning, conservation strategies, and the sustainable management of forest ecosystems under changing climatic conditions.

Keywords Climate change · MaxEnt · Habitat suitability · Western Turkey · *Pinus nigra* · *Pinus sylvestris* · *Abies nordmanniana* · *Quercus* spp. · *Fagus orientalis*

Introduction

Forest ecosystems play a critical role in regulating climate, maintaining biodiversity, and providing essential ecosystem services such as carbon sequestration, water regulation, and habitat provision (Cantarello et al. 2024). Tree species composition and distribution strongly influence forest structure, productivity, and resilience to environmental change. Understanding how dominant tree species respond to ongoing climate change is therefore fundamental for sustainable forest management, biodiversity conservation, and long-term ecosystem stability (Nardi et al. 2016). In this context, species distribution models (SDMs) have become widely used tools for assessing current and future species–environment relationships.

Building on this framework, SDMs are increasingly applied to estimate potential geographical distributions and species–environment relationships, particularly under climate change scenarios (Araújo et al. 2019; Pili et al. 2025). Climate change has a significant impact on the functioning of ecosystems and the distribution of species, and stands out as one of the main factors determining the habitat areas of plant taxa (Bertrand et al. 2011). Throughout the Earth’s 4.5 billion-year history, climate systems have constantly changed (Türkeş, 2008); however, it is known that climate change has accelerated in the last century and poses serious threats to natural ecosystems. According to the Fifth Assessment Report published by the Intergovernmental Panel on Climate Change (IPCC), the global average surface temperature increased by 0.85 °C between 1880 and 2012 (IPCC 2013). In the coming period, this temperature increase is expected to be between 0.3 °C and 1.7 °C (RCP2.6 scenario) or between 2.6 °C and 4.8 °C (RCP8.5 scenario) (IPCC, 2014). These changes bring critical problems such as habitat loss and extinction risk, especially for species with limited distribution (Thuiller et al. 2005; Lawler et al. 2009; Cobben et al. 2015; Ashraf et al. 2016; Yi et al. 2016; Zhang et al. 2018).

In this context, species distribution modeling studies play a critical role in predicting current and future distributions of plant species, identifying potential habitat losses, and developing conservation strategies for ecosystem management (Gaston and Blackburn 1996). The Maximum Entropy (MaxEnt) model is one of the most widely used modeling methods in this field and has been shown to provide strong predictive performance across different taxonomic groups and geographic regions (Phillips et al. 2006; Phillips and Dudík, 2008). The major advantages of MaxEnt include short modeling time, ease of use, the capacity to work with small sample sizes, and high prediction accuracy (Hernandez et al. 2006; Pearson et al. 2007). This model allows the determination of current and potential future distributions of species using bioclimatic data (WorldClim 2020) and coordinate data of the species’ observation points.

In various studies, distribution changes of different species were examined using the MaxEnt model and the effects of climate change were revealed. For example, Fyllas et al. (2022) evaluated the current and future habitat suitability of dominant tree species in Greece and found that taxa at high altitudes experienced habitat contraction. Bektaş et al. (2022) identified suitable habitats for the rare and threatened species *Xerophyllum asphodeloides* in Talladega National Forest, USA, and found that this area was only 159.57 ha. Remya et al. (2015) found that *Myristica dactyloides* in the Eastern Ghats Mountains of India will experience significant habitat loss in 2050 and 2070. Similarly, in Turkey, Çoban et al. (2020) modeled the future distribution of *Quercus libani* (Lebanese Oak) and determined that suitable areas will decrease by 67% by 2070. Uzun et al. (2020) emphasized

that the distribution areas of *Acer campestre* species will shrink and conservation strategies should be developed. In another study by Akyol and Örüçü (2019), it was shown that the most important factors affecting the habitat suitability of *Pinus pinea* (Pistachio Pine) are the minimum temperature of the cold month (Bio6), annual precipitation (Bio12) and the amount of precipitation in the wettest quarter (Bio16), and it was determined that the species will experience habitat loss in the future and shift further north and to higher altitudes.

Recent regional studies from the Middle East and neighboring regions demonstrate that both climate change and land-surface characteristics strongly control the spatial dynamics of forest and wetland species. Mirhashemi et al. (2024) investigated the combined effects of climate change and land-use change on the distribution of *Quercus brantii* forests using multiple species distribution models, including MaxEnt, under RCP 2.6 and RCP 8.5 scenarios, showing that climatic variables particularly temperature and precipitation seasonality were the dominant drivers of habitat suitability and that severe habitat losses are likely by 2070 under pessimistic scenarios. Similarly, Khwarahm (2025) modeled the potential distribution of the invasive species *Phragmites australis* in Iraq using MaxEnt under SSP1–2.6 and SSP5–8.5 scenarios (the SSP-based equivalents of RCP2.6 and RCP8.5), identifying land-cover types, wetlands, precipitation, and elevation as key conditioning factors and projecting a net decline in highly suitable habitats despite localized gains. Together, these studies indicate that species distributions in climatically sensitive Middle Eastern ecosystems are shaped by interacting climatic and land-surface controls, and that MaxEnt-based projections provide a valuable basis for conservation and management planning.

This study aims to determine the current and future horizontal and vertical distribution patterns of five dominant tree species (*Pinus nigra* Arn., *Pinus sylvestris* L., *Abies nordmanniana* subsp. *bornmülleriana* Mattf., *Fagus orientalis* Lipsky, and *Quercus* spp.) within the borders of the Western Black Sea Region of Turkey one of the country's most ecologically and economically significant forested areas. These species are not only vital components of regional forest ecosystems but also play key roles in providing essential ecosystem services such as water regulation, erosion control, carbon sequestration, and biodiversity support. Furthermore, they carry important socio-cultural and economic value: *Quercus* spp. holds symbolic meaning in Turkish culture, while *Fagus orientalis* is traditionally used in local architecture and crafts.

While habitat suitability modeling has been widely applied to assess the horizontal (geographic) distribution of tree species under climate change, very few studies have addressed their vertical (elevational) distributional shifts, and even fewer have explored the resulting changes in forest stand composition over time. This study fills a critical gap by modeling both horizontal and vertical distribution changes using MaxEnt software and bioclimatic data from WorldClim for the years 2030, 2050, 2070, and 2090 under different climate scenarios.

Moreover, it uniquely analyzes the future potential distribution and relative proportions of forest stand types (mixtures of species) for the years 2030 and 2090. By evaluating how the overlap of suitable habitats among species may evolve, this study provides a comprehensive assessment of potential stand-type compositions and their projected shifts under climate change. While previous studies have investigated species-level habitat changes, integrated analyses of multi-species stand-type dynamics at a regional scale remain limited, highlighting the added value of the present approach. Thus, this research provides robust

and policy-relevant insights for adaptive forest planning, species conservation, and sustainable forest management under climate change.

Material and method

Study area

For this study, the Western Black Sea Region of Turkey, specifically covering the provinces of Düzce and Bolu, was selected as the study area. Geographically, it is located between 30°29'00" and 32°38'00" E longitudes and 40°03'00" and 41°10'00" N latitudes (Fig. 1). The region spans from sea level up to 2400 m in altitude and covers a total area of 1,025,129 hectares, approximately 61% of which consists of forested land. Particularly, the Karadere, Seben, and Aladağ forests are very rich in terms of biodiversity and quality timber production. Turkey's first FSC-certified forests (Aladağ) are also located within this area. The Abant Mountains within the study area lie in the Euro-Siberian phytogeographic region and form a transition zone between the Euxine flora associated with the Black Sea coast and the Irano-Turanian floristic region associated with Central Anatolia (Köppen and Geiger 1954).

The study area experiences a continental climate. According to 30-year climate data averages, the average daily sunshine duration is 5.2 h, the average annual number of rainy days is 136, the average annual precipitation is 691 mm, and the average annual temperature is 10.5 °C (MGM, 2021). Broad-leaved tree species, such as *Fagus orientalis* (142,796 ha) and *Quercus* spp. (63,186 ha), are generally distributed at lower elevations, whereas coniferous

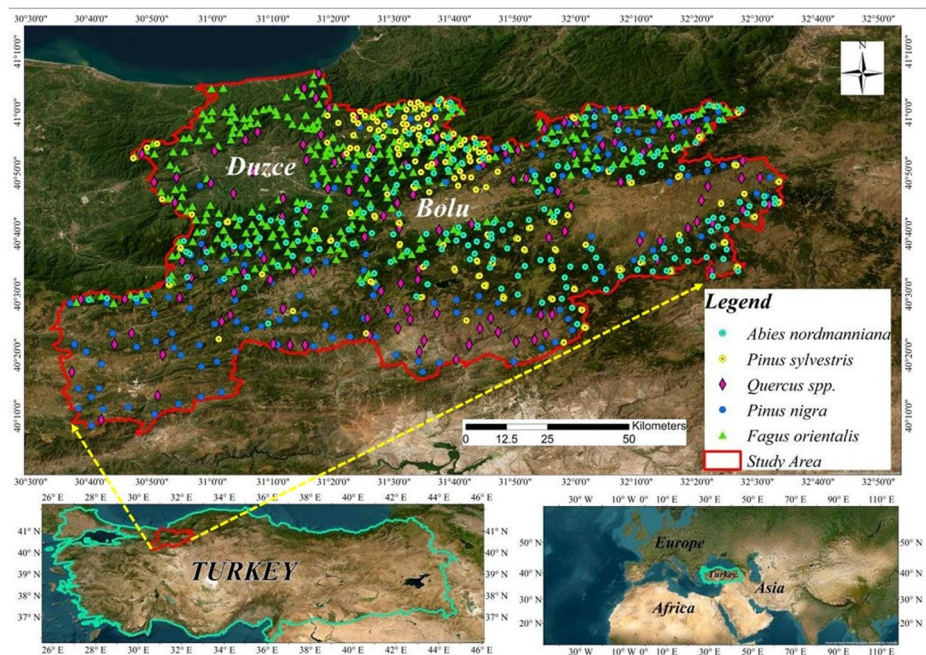


Fig. 1 The geographical location of the study area and occurrence data for tree species

species like *Pinus nigra* (237,894 ha), *Pinus sylvestris* (112,338 ha), and *Abies nordmanniana* (56,345 ha) are more dominant at higher altitudes. Data on pure stands consisting of single tree species and mixed stands containing the dominant tree species were obtained from forest management plans, and their distribution areas were recorded as point data (Fig. 1). The forest management plans for the forest enterprises within the study area were renewed in 2018. During the renewal process, systematic sampling was conducted at 300 × 300 m intervals, and stand types were determined by integrating ground-based measurements with satellite imagery across all forested areas. All stages of management plan development were supervised by public sector experts. Therefore, the stand type maps derived from the forest management plans were considered highly reliable for determining species occurrence points. In this study, the occurrence points of each tree species were obtained from the 2018–2020 forest management plan datasets of the General Directorate of Forestry (GDF), which include systematically sampled stand type maps based on 300 × 300 m grid intervals. In total, 2,350 occurrence points were used across five species (*Pinus nigra*: 540, *Pinus sylvestris*: 410, *Abies nordmanniana*: 370, *Fagus orientalis*: 520, *Quercus* spp.: 510). These data were field-verified and approved by GDF experts during the most recent management plan revision.

The ecological and climatic requirements of the tree species used in the study are of great importance. *Fagus orientalis* is a shade-tolerant species that generally prefers humid and cool climates at altitudes of 600–1500 m and grows in deep, humus and well-drained soils (Kuzugüdenli 2021). *Pinus sylvestris* is resistant to hot and dry summers and mild winters and grows well in sandy and slightly acidic soils with its drought-resistant structure in the 0–1000 m range (Ertuğrul and Bilir 2022). *Quercus* spp. grows in humid and warm climatic conditions at altitudes of 600–1500 m, prefers nutrient-rich, deep soils and is usually found in mixed forests (Kocabiyik et al. 2023). *Abies nordmanniana* grows in the 1000–2500 m range dominated by cold and humid climates and grows best in deep, humus and well-drained soils (Kuzugüdenli 2021). *Pinus nigra* (Larch), on the other hand, adapts to cold and dry climatic conditions at altitudes of 500–2000 m and grows well in acidic soils with its drought-resistant structure (Kocabiyik et al. 2023).

Environmental variables

The WorldClim 2.1 database published in 2020 was used to model the current potential distribution of each species. WorldClim 2.1 shows monthly minimum, maximum and average temperature, precipitation, wind speed, water vapor pressure, solar radiation and total precipitation data from 1970 to 2000. WorldClim climate datasets are calculated over long-term averages (such as 30 years) and since the years 2000–2020 do not yet constitute a 30-year period, the current datasets include data from 1970 to 2000. There are also 19 different bioclimatic data. Climatic data with a spatial resolution of 30 s (1 km²) were used to determine the current distribution range of the species (Fick and Hijmans 2017; WorldClim 2020). The use of a single high-performance GCM allowed for a high-resolution focused analysis (1 km²) consistent with the regional forest management data, although we acknowledge that multi-model ensembles represent the gold standard for quantifying climatic uncertainty. In addition, elevation, slope, and aspect maps of the study area were produced and used with bioclimatic data (Table 1). In this study, elevation data (1 km resolution) were down-

Table 1 All of the environmental variables used to construct the models and the variables used in the model (shown in grey scale)

Variable	Description	Unit
Bio1	Annual mean temperature	°C
Bio2	Mean diurnal range [mean of monthly (max temp–min temp)]	°C
Bio3	Isothermality (bio2/bio7) (* 100)	–
Bio4	Temperature seasonality (standard deviation * 100)	–
Bio5	Max temperature of warmest month	°C
Bio6	Min temperature of coldest month	°C
Bio7	Temperature annual range (bio5–bio6)	°C
Bio8	Mean temperature of wettest quarter	°C
Bio9	Mean temperature of driest quarter	°C
Bio10	Mean temperature of warmest quarter	°C
Bio11	Mean temperature of coldest quarter	°C
Bio12	Annual precipitation	mm
Bio13	Precipitation of wettest month	mm
Bio14	Precipitation of driest month	mm
Bio15	Precipitation seasonality (coefficient of variation: mean/sd*100)	%
Bio16	Precipitation of wettest quarter	mm
Bio17	Precipitation of driest quarter	mm
Bio18	Precipitation of warmest quarter	mm
Bio19	Precipitation of coldest quarter	mm
Elevation	Elevation	m
Aspect	Aspect	Degrees
Slope	Slope	%

loaded from GTOPO30 (<https://lta.cr.usgs.gov/GMTED2010>; Danielson and Gesch 2011) and aspect and slope maps were produced from this data.

To reduce multicollinearity among bioclimatic data, Variance Inflation Factor (VIF) (Marquardt 1970) analysis was applied to the data and bioclimatic variables with VIF values greater than 10 were excluded from the model. In this way, the environmental variables used in the model were reduced from 22 to 10 (Table 1). To determine the degree of contribution of environmental variables, the MaxEnt model Jackknife test was used (Pearson et al. 2007).

This study used the Pierre Simon Laplace Institute Climate Simulation Modeling (IPSL CM6A-LR), which uses mathematical equations to simulate the complex interactions of Earth's climate system. To predict future distributions of tree species with the MaxEnt model, the Coupled Model Intercomparison Project Phase 6 (CMIP6) scenarios developed by the IPCC in its 6th Report (<https://pcmdi.llnl.gov/CMIP6/>) were used. These scenarios are also referred to as 21st century scenarios. In the IPCC 6th report, the RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5 scenarios, which examine projected future greenhouse gas emissions, were updated and renamed Shared Socio-economic Pathways (SSPs) as SSP 1–2.6, SSP 2–4.5.5, SSP 4–6.0 and SSP 5–8.5. The SSP scenarios combine the RCP targets with the RCP scenarios to create four different pathways the world can take to address climate change. In fact, the SSP and RCP scenarios are designed to complement each other. Namely, RCP scenarios aim to estimate greenhouse gas concentrations and the amount of warming the world could achieve by the end of the century, while SSP scenarios predict whether emission-reduction targets can be met. (O'Neill et al. 2016; Carbonbrief 2018). Of the cli-

mate scenarios, SSP 1 is based on a world where sustainably-oriented growth, equality of peoples and human well-being is prioritized, SSP 2 is based on unbalanced development and income growth, SSP 4 is based on ever-increasing inequality, and SSP 5 is based on rapid and unconstrained growth in economic output and energy use (O'Neill et al. 2016; Carbonbrief 2018). In this study, SSP 2–4.5 and SSP 5–8.5 scenarios were used and data for the periods 2030 (2020–2040), 2050 (2041–2060), 2070 (2061–2080), and 2090 (2081–2100) were utilized. The current and future distribution areas of the species were determined for each scenarios using the MaxEnt model. Elevation data classified at 200 m intervals were used to determine the vertical distribution of the species. The IPSL-CM6A-LR global climate model was selected due to its documented performance in representing temperature and precipitation patterns over the Eastern Mediterranean and Anatolian region, as well as its frequent use in recent regional-scale climate impact and ecological modeling studies.

Model building

Species distribution models were developed using MaxEnt version 3.4.3 (Phillips et al. 2020), which estimates species–environment relationships based on presence-only data and background environmental conditions. For each species, occurrence records were randomly partitioned, with 75% of the data used for model training and 25% reserved for model testing. Model complexity was controlled using the default regularization multiplier ($\beta = 1$) and automatic feature selection, which have been shown to provide robust predictive performance while limiting overfitting for moderate sample sizes (Phillips and Dudík, 2008; Merow et al. 2013). For each species, 10,000 background points were randomly sampled by MaxEnt across the study area to characterize available environmental conditions, which is consistent with standard practice for regional-scale modeling. Background points were restricted to forested and potentially accessible areas defined by the forest management plan boundaries in order to avoid sampling environmentally unrealistic locations. No spatial bias file was applied because the occurrence data were derived from a systematic 300×300 m sampling grid, providing homogeneous spatial coverage across the study area.

Model evaluation

Receiver Operating Characteristic (ROC) and Area Under the ROC Curve (AUC) values were used to determine the performance of the MaxEnt Model (Wang et al. 2007; Phillips et al. 2017). The AUC represents the probability that a randomly selected presence location is ranked higher than a randomly selected background location. The AUC indicates the success of the model and if the $AUC > 0.5$, the model performs better than a random forecast (Phillips and Elith 2010). The MaxEnt model shows the probability of a species being found in a given location between 0 and 1. The probability value approaches 1 if the probability of the species being found in that area is high and 0 if it is low. Habitat suitability is a measure of how well a given area meets the environmental requirements of a species. In the MaxEnt model, habitat suitability is represented by the environmental variables used to model species distribution. Habitat density refers to the number of individuals of a species found in a given area. While areas with higher habitat suitability are generally expected to support higher species densities, other factors such as extinction debt and immigration credit can influence this relationship. Some habitats may still harbor high species densities despite

long-term unsuitability, while others may have low densities due to time lags in colonization, even if they offer high habitat quality. Although AUC was used as the primary metric to assess model performance, its limitations in presence-only modeling are acknowledged. Therefore, AUC values were interpreted comparatively among species and scenarios rather than as absolute indicators of predictive accuracy. This evaluation strategy is consistent with previous regional-scale MaxEnt applications where comparative model performance across species and scenarios is prioritized. Because true absence data were not available, threshold-dependent metrics such as Kappa or TSS were not used, as they can artificially inflate model accuracy when pseudo-absences are applied.

MaxEnt model results were converted into distribution maps using ArcGIS 10.4TM software. ASCII (asc) outputs generated by MaxEnt were converted into vector format for subsequent spatial analyses. The Maximum Training Sensitivity plus Specificity (MTSPS) threshold was used only for binary presence–absence classification and area calculations, ensuring an objective and species-specific delineation of suitable habitat. Fixed threshold values were subsequently applied only to classify relative habitat suitability levels for comparative interpretation. Accordingly, areas with suitability values lower than 0.5 were classified as ‘not suitable’, values between 0.5 and 0.75 as ‘suitable’, and values greater than 0.75 as ‘very suitable’ potential habitats (Engler et al. 2004; Baldwin 2009; Li et al. 2014). These fixed thresholds were not used for model evaluation or validation purposes. In addition, ArcGIS 10.4TM software was used to determine the vertical distribution densities of tree species under the SSP 2–4.5 and SSP 5–8.5 scenarios. Vertical distribution density was classified as ‘low’ ($\leq 5,000$ ha), ‘medium’ (5,000–20,000 ha), ‘high’ (20,000–30,000 ha), and ‘very high’ ($> 30,000$ ha) based on the total distribution area of each species within the corresponding elevation band and time period.

Results

MaxEnt species distribution model results

As a result of this study, the Area Under the Curve (AUC) values, which indicate the predictive performance of the model, were found to be 0.991 (± 0.001) for *Pinus nigra*, 0.993 (± 0.001) for *Pinus sylvestris*, 0.990 (± 0.001) for *Abies nordmanniana*, 0.986 (± 0.001) for *Fagus orientalis*, and 0.991 (± 0.001) for *Quercus spp.*, using Receiver Operating Characteristic (ROC) curves (Fig. 2). The AUC value, ranging from 0 to 1, measures the model’s ability to distinguish between suitable and unsuitable habitats, with values closer to 1 indicating higher predictive accuracy. According to these results, all AUC values are significantly higher than 0.5, which represents a random model, suggesting that the model performs well in distinguishing suitable and unsuitable habitats under current conditions. These high AUC values indicate strong discriminatory capacity of the MaxEnt models under current conditions; however, they should be interpreted with caution, as model evaluation was based on random training–testing data partitioning rather than fully spatially independent validation. According to the results of the Jackknife test of variable importance, precipitation of the driest month (Bio14), temperature seasonality (Bio4), and isothermality (Bio3) played the main roles in modeling all tree species among the bioclimatic variables.

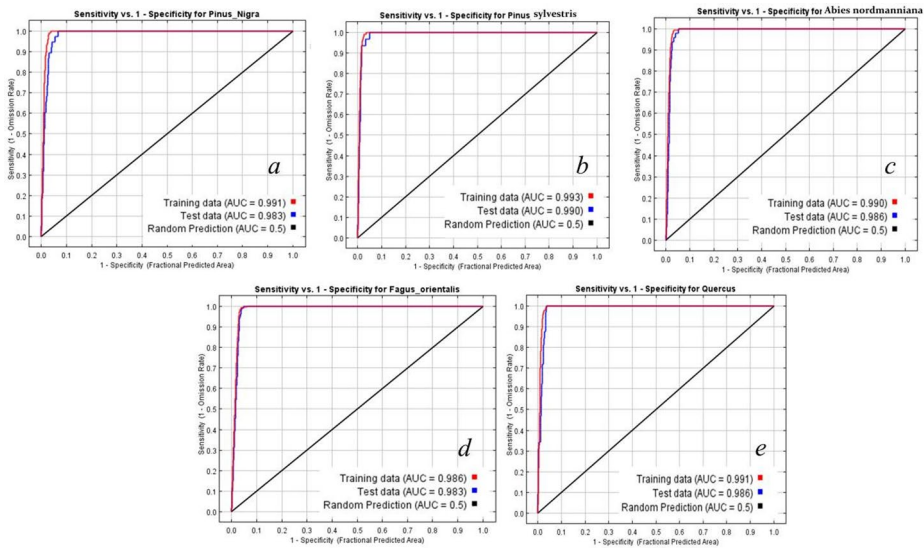


Fig. 2 ROC curves and AUC for MaxEnt models under current conditions **a** *Pinus nigra*, **b** *Pinus sylvestris*, **c** *Abies nordmanniana*, **d** *Fagus orientalis*, **e** *Quercus* spp.

To validate the model under current climate conditions, predicted habitat suitability maps were compared with actual species distribution data derived from the 2018–2020 forest management plans. The overlap ratio between predicted suitable areas (suitability > 0.5) and actual occurrence areas exceeded 85% for all species, indicating strong model reliability. The mean AUC value for all species (0.990 ± 0.003) further confirms the excellent predictive performance of the MaxEnt models under current climate conditions (Fig. 2). In addition, the comparison between modeled and observed distributions showed a high degree of consistency for all taxa, with *Quercus* spp. and *Fagus orientalis* exhibiting the highest agreement (approximately 89% and 88%, respectively), followed by *Pinus nigra* and *Pinus sylvestris* (both around 87%). *Abies nordmanniana* presented a slightly lower correspondence (around 86%), likely due to its restricted altitudinal range and sensitivity to local climatic variations. Overall, these findings demonstrate that the MaxEnt models successfully capture the present spatial patterns of all five species, providing a solid foundation for projecting their potential future distributions under different climate scenarios.

Vertical distribution of tree species according to SSP 2–4.5 and SSP 5–8.5 scenarios

The vertical distribution of the current and future status of the tree species and their distribution densities were evaluated according to the SSP 2–4.5 and SSP 5–8.5 scenarios results on the basis of suitable and very suitable distribution areas. According to the SSP 2–4.5 scenario, it is predicted that *Pinus sylvestris*, which has a limited distribution up to 2200 m altitude, will leave its distribution area in 2050 and *Abies nordmanniana* will leave its distribution area at this altitude in 2030. In 2090, it is thought that *Pinus sylvestris* species will begin to spread slightly at an altitude of 400–600 m. According to this scenario, *Pinus sylvestris*, *Pinus nigra* and *Abies nordmanniana* species are predicted to be intensively dis-

tributed in all periods, especially at 800–1600 m altitudes. *Abies nordmanniana* tree species is predicted to lose their distribution areas above 2000 m in 2070. *Quercus* spp. species are expected to be intensively distributed between 600 and 1400 m and *Fagus orientalis* species between 600 and 1600 m altitudes (Fig. 3a). According to the SSP 2–4.5 model, when the vertical distribution of very suitable areas for tree species is examined, it is estimated that there will be no very suitable areas for any tree species above 2000 m, and that *Pinus sylvestris* will spread at an altitude of 2000 m, albeit limited. All tree species are predicted to have moderate to dense distributions generally at 800–1600 m altitudes. According to the SSP 2–4.5 model, *Quercus* spp. and *Pinus nigra* species are predicted to have the densest distributions in terms of very suitable distribution areas (Fig. 3b).

According to the SSP 5–8.5 scenario, when the changes of suitable and very suitable distribution areas for tree species according to elevation are examined, it is seen that suitable areas for species are distributed up to a maximum of 2200 m. According to this scenario, the highest altitudes are also predicted to be abandoned in short periods. *Pinus sylvestris* is predicted to lose its distribution area at 2200 m altitude by 2050 and *Abies nordmanniana* by 2030. *Fagus orientalis* and *Quercus* spp. species seem to increase their weak distribution density at lower elevations. The highest densities for *Fagus orientalis* and *Quercus* spp. are predicted to occur at altitudes between 800 m and 1400 m, while other coniferous species

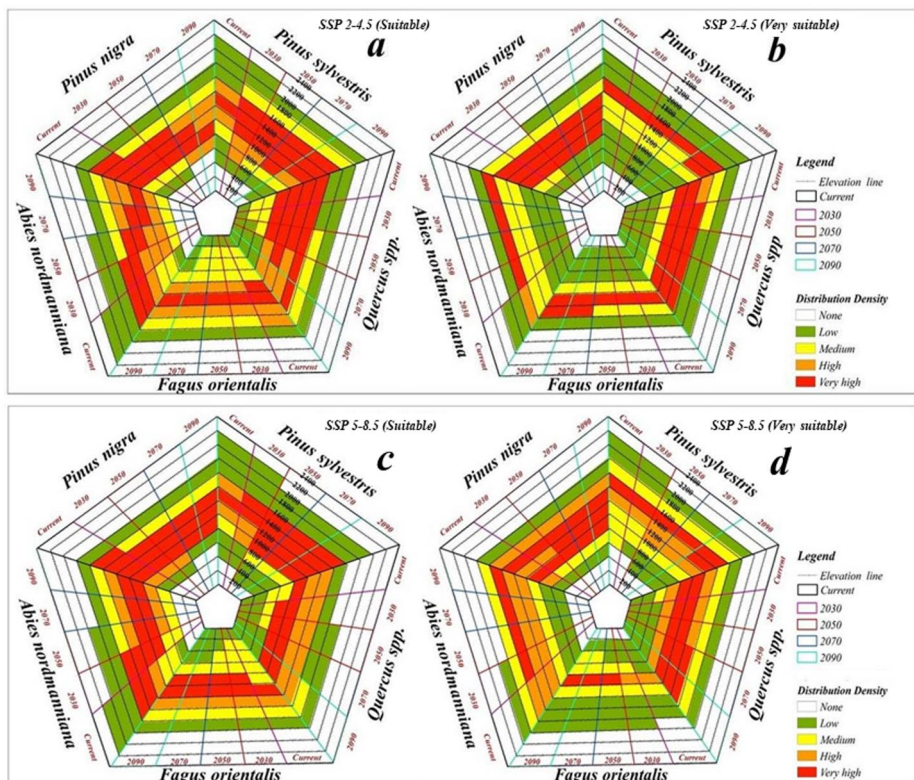


Fig. 3 Vertical distribution densities of species under SSP 2–4.5 and SSP 5–8.5 scenarios: **a** suitable areas (SSP 2–4.5), **b** very suitable areas (SSP 2–4.5), **c** suitable areas (SSP 5–8.5), and **d** very suitable areas (SSP 5–8.5)

are predicted to have their highest densities between 800 m and 1600 m (Fig. 3c). The SSP 5–8.5 scenario predicts that only *Pinus sylvestris* will spread up to 2200 m in the vertical distribution of areas that are very suitable for tree species. In 2050, it is seen that *Pinus sylvestris* will also prefer lower altitude areas. According to this scenario, *Abies nordmanniana*, which spreads up to 2000 m, is predicted to lose its distribution area at this altitude in 2050. According to the SSP 5–8.5 scenario, *Fagus orientalis* has no distribution area at 0–200 m in terms of very suitable areas and is expected to spread at an altitude of 1800 m by 2030, albeit at low density. According to this scenario, *Abies nordmanniana* and *Pinus sylvestris* are predicted to spread between 1000 and 1600 m, *Pinus nigra* 800–1600 m, *Quercus* spp. 600–1400 m and *Fagus orientalis* between 800 and 1000 m in terms of the densest distribution areas (Fig. 3d).

Horizontal distribution of tree species according to SSP 2–4.5 and SSP 5–8.5 scenarios

According to the MaxEnt results of the SSP 2–4.5 scenario, *Pinus nigra* and *Quercus* spp. are the highest horizontal distribution. According to this scenario, it is estimated that *Quercus* spp. will increase its possible distribution areas in the future and approximately 41% of the whole area will be very suitable for *Quercus* spp. The increase in the very suitable areas of *Quercus* spp. shows that especially the areas that are suitable from the spreading areas are transformed into very suitable areas (Fig. 4a). While no change is expected in the suitable areas of *Pinus nigra*, it is predicted that there will be a contraction in the very suitable areas (Fig. 4b). For *Abies nordmanniana* and *Fagus orientalis*, it is expected that there will be a small shrinkage in the suitable distribution areas and a slight increase in the very suitable distribution areas (Fig. 4c, d). For the *Pinus sylvestris*, an increase of about 7% is expected in very suitable areas and a decrease of about 2% in suitable areas (Fig. 4e) (Table 2).

According to the MaxEnt results of for the SSP 5–8.5 scenario, when the horizontal distribution of tree species is analyzed, it is seen that there is a similar distribution to the SSP

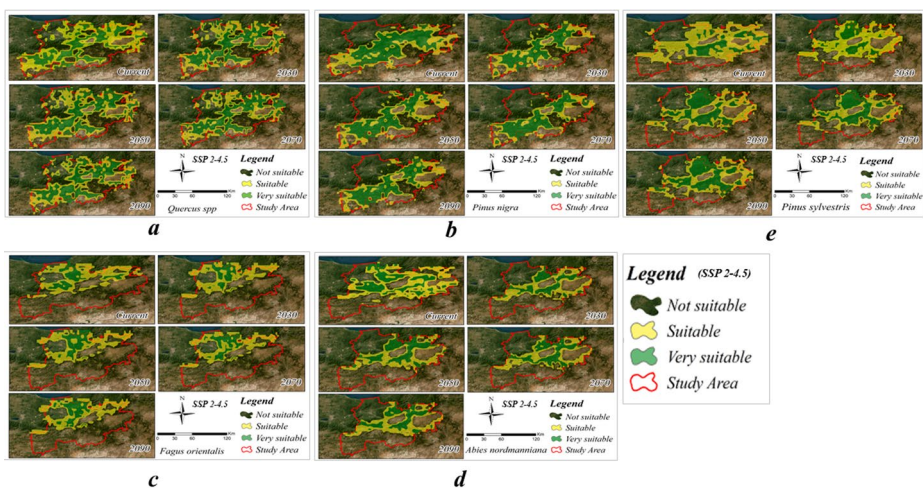


Fig. 4 Spatial distribution of dominant tree species under the SSP 2–4.5 scenario: **a** *Quercus* spp., **b** *Pinus nigra*, **c** *Fagus orientalis*, **d** *Abies nordmanniana*, and **e** *Pinus sylvestris*

Table 2 Horizontal distribution of tree species according to maxent results of SSP 2–4.5 scenario

SSP 2–4.5		Current		2030		2050		2070		2090	
Tree species	Suitability	Area (ha)	%	Area (ha)	%	Area (ha)	%	Area (ha)	%	Area (ha)	%
<i>Pinus sylvestris</i>	Suitable	254765.8	24.9	220254.0	21.5	228298.1	22.3	227165.1	22.2	235882.3	23.0
	Very suitable	225884.1	22.0	249779.3	24.4	282735.1	27.6	283015.2	27.6	299132.8	29.2
<i>Pinus nigra</i>	Suitable	190694.0	18.5	174328.0	17.0	179761.7	17.5	182318.4	17.8	188062.8	18.3
	Very suitable	370878.0	36.2	319000.0	31.1	323200.6	31.5	320031.0	31.2	327364.1	31.9
<i>Abies nordmanniana</i>	Suitable	214147.5	20.9	226099.6	22.1	217364.0	21.2	198663.6	19.4	198134.6	19.3
	Very suitable	230232.8	22.5	232972.2	22.7	235553.6	23.0	246906.4	24.1	246981.2	24.1
<i>Quercus</i> spp.	Suitable	265913.6	25.9	255000.1	24.9	250273.6	24.4	210696.7	20.6	203179.1	19.8
	Very suitable	363532.1	35.5	378199.9	36.9	382081.9	37.3	388655.6	37.9	418888.4	40.9
<i>Fagus orientalis</i>	Suitable	218186.0	21.3	220340.3	21.5	214398.7	20.9	199831.5	19.5	210540.0	20.5
	Very suitable	113127.0	11.0	113401.8	11.1	111534.8	10.9	120331.5	11.7	128809.9	12.6

Area calculations (ha) and percentage values (%) are based on the Maximum Training Sensitivity plus Specificity (MTSPS) threshold to ensure species-specific objective delineation

2–4.5 scenario and especially *Quercus* spp. and *Pinus nigra* are spread in the largest areas (Fig. 5). In particular, *Quercus* spp. is expected to increase by about 5% in very suitable areas and decrease by about 6% in suitable areas. *Pinus nigra* tree are expected to decrease by 6% in suitable areas and by approximately 4% in very suitable areas. *Abies nordmanniana* is predicted to have a 5% increase in suitable areas and a 2.3% increase in very suitable areas (Fig. 5a–b–c). As in the SSP 2–4.5 scenario, *Fagus orientalis* appears to be the least affected species according to the scenarios (Fig. 5d). The suitable areas of *Pinus sylvestris* are estimated to decrease by 4.5%, while the very suitable areas are estimated to increase by 3.2% (Fig. 5e), (Table 3).

When the spatial distribution of the species is examined according to the scenario results, it is seen that in both scenarios, the distribution of *Pinus sylvestris* increases from very suitable to suitable spreading areas and spreads towards the Abant Mountains. In both scenarios, the *Pinus nigra* is predicted to leave its distribution areas in the Abant Mountains and Bolu Mountains over the years and spread towards the more arid inland regions. *Abies nordmanniana* is predicted to maintain its spatial distribution areas in both scenarios. *Quercus* spp. are predicted to increase their distribution especially towards the north and northwest of Düzce. According to the SSP 2–4.5 scenario, *Quercus* spp. is predicted to have a higher distribution area in Düzce region. Although *Fagus orientalis* maintain their distribution areas in both scenarios, it is predicted that their very suitable distribution areas will be relatively more in the SSP 2–4.5 scenario.

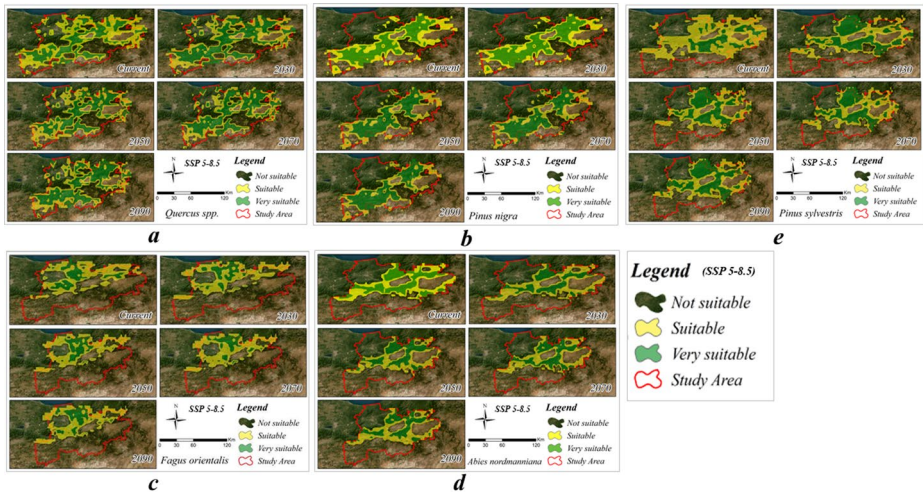


Fig. 5 Spatial distribution of dominant tree species under the SSP 5–8.5 scenario: **a** *Quercus* spp., **b** *Pinus nigra*, **c** *Fagus orientalis*, **d** *Abies nordmanniana*, and **e** *Pinus sylvestris*

Table 3 Horizontal distribution of tree species according to SSP 5–8.5 scenario maxent results

SSP 5–8.5	Suitability	Current		2030		2050		2070		2090	
Tree species		Area (ha)	%	Area (ha)	%	Area (ha)	%	Area (ha)	%	Area (ha)	%
<i>Pinus sylvestris</i>	Suitable	254765.8	24.8	225569.2	22.0	223664.9	21.8	219409.7	21.4	208225.6	20.3
	Very suitable	225884.1	22.0	241186.3	23.5	230547.0	22.5	227864.8	22.2	258708.3	25.2
<i>Pinus nigra</i>	Suitable	190694.0	18.5	147636.1	14.4	137396.4	13.4	130276.5	12.7	130925.9	12.8
	Very suitable	370878.0	36.2	332965.5	32.5	336585.2	32.8	326967.9	31.9	330395.0	32.2
<i>Abies nordmanniana</i>	Suitable	214147.5	20.9	249174.8	24.3	241569.3	23.6	248347.8	24.2	265316.2	25.9
	Very suitable	230232.8	22.5	264625.7	25.8	257772.3	25.1	258310.3	25.2	254536.1	24.8
<i>Quercus</i> spp.	Suitable	265913.6	25.9	217636.9	21.2	200273.9	19.5	206151.5	20.1	199000.3	19.4
	Very suitable	363532.1	35.5	392657.0	38.3	399984.4	39.0	401887.6	39.2	407677.8	39.8
<i>Fagus orientalis</i>	Suitable	218186.0	21.3	217071.0	21.2	219202.8	21.4	229379.8	22.4	212489.0	20.7
	Very suitable	113127.0	11.0	105949.4	10.3	119798.7	11.7	118079.2	11.5	127999.3	12.5

Area calculations (ha) and percentage values (%) are based on the MTSPS threshold to ensure species-specific objective delineation

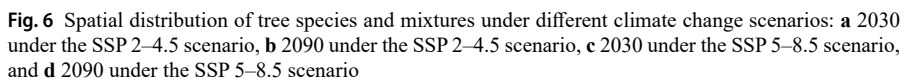
Potential forest stand compositions shaped by future species distributions

Based on the horizontal and vertical distributions obtained according to the SSP 2–4.5 and SSP 5–8.5 scenarios, possible future tree species mixes were determined from the data for 2030 and 2090. Tree species symbols used in forest management plans in Turkey were used to indicate stand types and mixtures. *Pinus nigra* is denoted by “Çk”, *Pinus sylvestris* by “Çs”, *Abies nordmanniana* by “G”, *Fagus orientalis* by “Kn” and *Quercus* spp. by “M”. According to the SSP 2–4.5 scenario, unsuitable areas for tree species are expected to decrease by about 52.0 km² by 2090. From 2030 to 2090, there will be a transition of 174.62 km² from unsuitable areas to areas with pure distribution of M tree species. It is estimated that there will be a decrease of approximately 150.0 km² in the distribution areas of pure Çk tree species and 94.6 km² of area, where Çk is distributed, will become unsuitable for species in 2090. While no significant change is expected in the areas of pure G and pure Kn tree species, pure M is expected to decrease by about 60.0 km². It is foreseen that 117.2 km² of ÇsG mixed stands will turn into pure Çs stands and 90.0 km² of KnG stands will turn into ÇsKnG mixed stands and Çs species will enter the mix. In 2090, 142.38 km² will enter the mix of Çs stands and 126.54 km² of Çs tree species will leave the mix of MÇsÇk stands. It is estimated that 91.08 km² of the MKnG mix will be converted into KnG stands where the M tree species will be removed. Potential stand mixes in 2030 (Fig. 6a), potential stand mixes in 2090 (Fig. 6b).

According to the results of the SSP 5–8.5 scenario, when the possible mixtures and transitions of tree species for the years 2030 and 2090 are analyzed, it is estimated that the amount of unsuitable area for all species will decrease by approximately 112.7 km². In this decrease, especially the M tree species increasing their distribution areas as pure M stands in unsuitable areas was effective. In addition, it is predicted that there will be transitions from areas where M, Kn, Çk, Çs and G species are pure to unsuitable areas. The highest transition to unsuitable areas will occur from pure M stands with 119.1 km² and pure Çk stands with 94.7 km². It is estimated that 117.2 km² of the ÇsG mixed stand will be transformed into a pure Çs stand, while 41.2 km² will be transformed into a ÇsÇkG stand by mixing with Çk. Çk will enter the mix in an area of 90.0 km² from the KnG stand. In 142.4 km² of the MÇk mixed stand, the Çs tree species is also included in the mixture, while in 126.5 km² of the MÇsÇk stand, the Çs tree species moves away from the area. It is predicted that M tree species will leave the distribution area in 91.1 km² of MKnG mixed stands. It is estimated that 79.4 km² of the MKnÇsG mixed stands will be converted to KnÇsG and M will leave the mixture. Potential stand mixes in 2030 (Fig. 6c), potential stand mixes in 2090 (Fig. 6d).

Discussion

This study utilized the MaxEnt model to assess the current and future distribution of five dominant tree species in the Western Black Sea Region of Turkey, under different climate scenarios. The findings underscore the pivotal role of bioclimatic variables, including dry month precipitation (Bio14), temperature seasonality (Bio4), and isothermality (Bio3), in shaping habitat suitability predictions for all species considered. These variables are essential in understanding how climate change affects species distributions, as they directly influence the ecological conditions required for optimal growth and survival. The significant



The dominance of temperature seasonality (Bio4), precipitation of the driest month (Bio14), and isothermality (Bio3) highlights the strong sensitivity of the studied tree species to thermal variability and seasonal water stress. Temperature seasonality reflects the magnitude of annual temperature fluctuations and is particularly important for montane and temperate forest species, where physiological tolerance thresholds may constrain growth and regeneration. Increased seasonality can potentially elevate frost damage risk in winter and heat stress during summer, thereby reducing habitat suitability in certain areas. Precipitation of the driest month represents moisture availability during the most critical period for plant survival and is closely associated with drought stress, especially for species with shallow root systems or high transpiration demands. Isothermality integrates daily and annual temperature variability and provides insight into climatic stability, which is often linked to the persistence of species with relatively narrow ecological niches. For example, increasing temperature seasonality (Bio4) can amplify frost damage in winter and heat stress in

summer, thereby constraining cambial activity and seedling establishment, particularly for cold-adapted species such as *Abies nordmanniana* and *Pinus sylvestris*. Similarly, low precipitation during the driest month (Bio14) increases drought stress, which limits physiological performance and survival at lower elevations. The strong effect of isothermality (Bio3) further indicates that climatic stability, rather than mean temperature alone, is critical for long-term habitat persistence in this transitional climatic zone.

Taken together, the prominence of these variables suggests that projected shifts in species distributions are likely to be strongly associated with increasing climatic variability and seasonal extremes, rather than changes in mean climate conditions alone. This interpretation is consistent with regional and global studies indicating that forest tree species responses to climate change are frequently mediated by drought intensity and temperature variability, particularly in transitional climatic zones such as the Western Black Sea region.

The MaxEnt model's high sensitivity and descriptive power were evident in its ability to predict significant shifts in species distributions under both the SSP 2–4.5 and SSP 5–8.5 climate scenarios. These scenarios represent contrasting levels of future greenhouse gas emissions, with SSP 5–8.5 predicting the highest emissions, likely resulting in more dramatic ecological shifts. The projections revealed notable changes in vertical and horizontal distribution patterns. High-altitude species like *Pinus sylvestris* and *Abies nordmanniana* are expected to experience substantial range contraction, with the former predicted to abandon its high-altitude habitats (2000–2200 m) by 2050, and the latter by 2030. This suggests that these species are highly sensitive to warming temperatures and may be unable to survive in their current high-altitude habitats as the climate warms.

In contrast, species such as *Pinus nigra* and *Quercus spp.* are projected to expand their horizontal distributions, particularly in lower altitudes (800–1600 m). This shift is indicative of the ability of these species to tolerate higher temperatures and potentially more arid conditions, a characteristic that could enhance their persistence in the face of climate change. From a management and conservation perspective, MaxEnt-based habitat suitability projections provide a powerful spatial framework for identifying priority zones for monitoring, assisted regeneration, and conservation planning under climate change. However, these models represent potential climatic suitability rather than realized species distributions, as they do not explicitly account for dispersal constraints, biotic interactions, or management interventions. Recent studies using MaxEnt and related species distribution models have demonstrated that these tools are highly effective for identifying priority conservation and management zones under climate change, particularly when combined with GIS-based spatial analyses and field data. However, they also highlight that model outputs represent potential climatic suitability rather than realized distributions and should therefore be interpreted cautiously when defining protected areas, restoration priorities, and management interventions (Hama and Khwarahm 2023; Radha and Khwarahm 2022; Majeed et al. 2023). From a management perspective, these projections identify altitudinal belts and landscape zones where species turnover and local extinction risk are most likely to occur, thereby providing a spatial basis for prioritizing monitoring, assisted regeneration, and adaptive silvicultural strategies.

A particularly intriguing result from this study is the contrasting trends in habitat suitability for different species. *Pinus nigra*, despite its potential horizontal expansion, is expected to experience a decline in the overall area of suitable habitat. This may reflect the combined effects of both temperature and precipitation changes, which could make some regions less

hospitable for the species. In contrast, *Pinus sylvestris* and *Quercus spp.* are projected to see increases in highly suitable areas, particularly in humid regions such as the Bolu and Abant Mountains. This suggests that *Pinus sylvestris*, which thrives in cooler and more temperate conditions, might benefit from the shifting climate patterns in certain regions, while *Quercus spp.*, with its broader tolerance to temperature variations, may gain ground as it adapts to changing conditions.

For *Fagus orientalis*, the model predicts a shift toward lower altitudes (600–1200 m) and an increase in highly suitable areas, although moderately suitable zones may decline. This finding aligns with previous studies by Ayan et al. (2022) and Yalçın (2012), who projected a contraction of *Fagus orientalis* in southern Turkey due to warming temperatures but an expansion in the Western Black Sea region. This suggests that *Fagus orientalis* is likely to experience some degree of adaptation to lower altitudes, potentially opening new opportunities for forest regeneration and the establishment of new populations in these areas.

One of the most striking findings of the study was the adaptability of *Quercus spp.* to a wide range of environmental conditions, which could help explain its broader distribution across different altitudes. This species' ability to coexist in both low-altitude areas dominated by *Fagus orientalis* and high-altitude regions inhabited by *Pinus nigra* highlights its resilience to climate change, a characteristic that may give it a competitive advantage over other species. Its greater tolerance to temperature variations could also allow it to persist and thrive in shifting climatic conditions, making it a key species for forest management and conservation in the region.

Additionally, the study examined the implications of pure versus mixed stands on carbon storage, an important consideration in forest management and climate change mitigation. The findings suggest that pure stands, particularly those of *Quercus spp.* and *Pinus sylvestris*, have higher carbon storage capacities due to their macro-aggregate soil structures, which facilitate more efficient carbon absorption. This is consistent with the findings of Shi et al. (2018) and Zhang et al. (2022), who demonstrated that pure stands are generally more effective in carbon sequestration compared to mixed stands. Interestingly, the SSP 5–8.5 scenario, which predicts higher carbon emissions, resulted in an increase in the area of pure stands, possibly reflecting their enhanced capacity to store carbon in the face of increased atmospheric carbon levels. This could have important implications for forest management, as promoting pure stands of these carbon-storing species may help mitigate the effects of climate change by enhancing forest carbon sequestration potential.

In conclusion, this study underscores the vulnerability of high-altitude species like *Pinus sylvestris* and *Abies nordmanniana* to climate change, with projections indicating significant shifts in their distribution patterns. However, it also highlights the resilience of *Quercus spp.*, which appears well-suited to adapt to climate change through its broader ecological tolerance. The potential for *Fagus orientalis* to shift to lower altitudes further underscores the dynamic nature of species distributions in response to climate change. These findings provide essential insights for sustainable forest management and conservation strategies, as they emphasize the importance of considering both bioclimatic variables and species-specific responses when planning for the future of forest ecosystems in the Western Black Sea region. Future research should explore additional modeling techniques, including the incorporation of biotic interactions, land use changes, and genetic adaptation factors, to refine predictions and support more effective conservation strategies.

Limitations and future directions

Although the MaxEnt model provided robust and spatially consistent predictions, several limitations should be acknowledged. First, this study focused solely on climatic and topographic variables, without incorporating potential biotic interactions, land-use dynamics, or soil related constraints that may influence future species distributions. The model also assumes species–climate equilibrium and does not account for dispersal limitations or adaptive capacity, which could affect species' ability to track shifting climatic niches. Moreover, the spatial resolution of the climatic data (1 km²) may overlook microclimatic variations in heterogeneous mountain landscapes such as the Western Black Sea region. Future research should integrate additional ecological factors (e.g., soil type, disturbance regimes, competition) and employ ensemble modeling or dynamic vegetation models to enhance prediction accuracy and ecological realism. Despite these limitations, the results presented here provide valuable insights for guiding adaptive forest management and conservation under changing climate conditions.

Model performance metrics, particularly AUC values, may be inflated due to the use of random training–testing data splits rather than spatially independent cross-validation. Occurrence records were derived from systematic forest inventory datasets, which may introduce spatial autocorrelation between training and test samples. While this systematic approach ensures comprehensive coverage, the 300 m interval was considered sufficient to capture the environmental heterogeneity of the Western Black Sea region's complex topography, thereby minimizing the impact of fine-scale spatial autocorrelation on model performance. Therefore, AUC values primarily reflect internal model consistency under current climatic conditions rather than true spatial transferability. Future studies should apply spatial block cross validation or independent regional datasets to provide more conservative and robust estimates of model performance.

Future projections in this study were based on a single CMIP6 global climate model (IPSL-CM6A-LR) and therefore do not explicitly capture inter model climate uncertainty. While this approach ensures internally consistent comparisons across scenarios and time periods, it may underestimate the full range of possible future climatic conditions. Ensemble-based projections using multiple CMIP6 models would be required to better quantify uncertainty bounds and improve the robustness of future habitat suitability estimates. Although MaxEnt is well suited for identifying climatically suitable areas, it does not explicitly represent demographic processes, dispersal constraints, or competitive interactions. Therefore, suitability maps should be interpreted as indicators of relative climatic favorability rather than direct predictions of future forest composition, and they should be integrated with forest inventory data and management planning to avoid misinterpretation.

Conclusions

The results obtained from the MaxEnt model and climate projections provide insights into potential future shifts in the spatial distribution of major tree species. Climate change scenarios have profound implications for the ecological requirements of species, leading to significant shifts in their distribution areas. Habitat suitability models, such as the MaxEnt model used in this study, serve as vital tools for predicting current and future species dis-

tributions, offering critical insights for conservation and management strategies. This study focused on the Western Black Sea region of Turkey, a key forestry area, to analyze the distribution patterns of five dominant tree species under two distinct climate scenarios. Given that this region is one of Turkey's most intensive wood production areas, it is imperative to prioritize forest conservation, sustainable management, and proactive measures to mitigate future habitat loss. Controlled wood production, afforestation using locally adapted tree species, and strict enforcement against illegal logging and overgrazing are essential steps to safeguard these forests.

While environmental variables such as temperature and precipitation are critical in predicting species distributions, they do not fully capture the complexity of ecological dynamics. Anthropogenic factors, biotic interactions, and regional growing conditions must also be considered to enhance the accuracy of distribution models. Furthermore, genetic diversity studies should be conducted to improve species' adaptability to changing climatic conditions. Activities that disrupt rainfall and temperature regimes such as deforestation, unsustainable agricultural practices, and water pollution must be minimized to protect natural ecosystems and maintain species distributions.

To ensure the long-term sustainability of forests in the region, integrated planning and decision-making processes are crucial. Measures such as promoting sustainable forestry practices, protecting water resources, and implementing eco-friendly agricultural methods can mitigate negative climate impacts and preserve the natural distribution of tree species. Future research should explore the integration of additional modeling techniques and parameters to develop more robust and region-specific models.

In conclusion, understanding the potential future distribution of tree species based on their current status is essential for guiding conservation efforts and ensuring the sustainability of forest ecosystems. By combining scientific modeling with proactive management and policy interventions, we can better address the challenges posed by climate change and protect the ecological integrity of critical forest regions like the Western Black Sea region.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors and are aware that with minor exceptions, no changes can be made to authorship once the paper is submitted.

Consent to participate Not applicable.

Consent for publication Not applicable.

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