

Climate change drives elevational gradients in *Sorbus domestica* L. habitat

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Abstract

Climate change poses a significant threat to biodiversity, influencing habitat distribution and survival of forest tree species. The True Service Tree (*Sorbus domestica* L.), a temperate species with ecological and economic importance, faces uncertain prospects for adaptation under future climate conditions. This study utilizes species distribution models (SDMs) and various environmental variables to assess shifts in habitat distribution and migration trends under current and future climate scenarios (SSP2-4.5 and SSP5-8.5). Results indicate that under the extreme SSP5-8.5 scenario, the average altitude of suitable habitats could rise by approximately 160 meters by 2100, highlighting potential migration to higher altitudes as an adaptation to habitat loss pressures. However, it remains uncertain whether this upward shift can keep pace with the rapid rate of climate change. Additionally, the study identifies the mean temperature of the driest quarter as a critical limiting factor for habitat suitability, underscoring temperature's pivotal role in shaping the species' future distribution. By integrating climate, landscape, and elevation variables, the study quantifies the relative importance of various environmental factors in determining species distribution across different climate scenarios. Including landscape variables such as soil organic carbon, land cover type, and clay content significantly improved model accuracy, emphasizing their influence on habitat quality and plant survival. This research provides a scientific basis for the conservation of *S. domestica* under future climate conditions, offering practical for reserve planning and habitat management. By addressing gaps in understanding the high-altitude migration adaptations of temperate forest tree species, the study also provides valuable insights for conserving other forest species, advancing climate-adaptive conservation strategies for biodiversity.

1. Introduction

Global climate change significantly affects the suitable habitats of species and biological communities (Bellard et al., 2012; Parmesan and Yohe, 2003). Human activities have undeniably intensified global warming through greenhouse gas (GHG) emissions, causing global surface temperatures from 2011 to 2020 to rise by 1.1°C compared to pre-industrial levels (1850–1900) (Lee et al., 2023). Between 1970 and 2010, CO₂ emissions from fossil fuel use and industrial activities accounted for approximately 78% of all GHG emissions (Pachauri et al., 2014). Climate change has also triggered extreme weather events including droughts and floods, directly harming biodiversity and ecosystems (Lee et al., 2023). Rising global temperatures increase the risk of species extinction, with an estimated 7.9% of species potentially facing extinction due to climate change. (Urban, 2015). Under current GHG emission trends, approximately one-sixth of global species are projected to be threatened (Urban, 2015). Warming temperatures have led to shifts in species habitats, as climate change not only alters global temperature and precipitation gradients but may also exceed species' physiological tolerance limits, thereby reducing the extent of suitable habitats. These habitat range shifts influence the fundamental niche—the maximum geographic range a species can occupy under ecological constraints, excluding biotic interactions (Colwell and Rangel, 2009).

Trees are under immense stress from climate change. Persistent global climate change, including rising CO₂ levels and reduced precipitation, profoundly impacts plant photosynthesis, phenology, nutrient composition, and phenotypes (Chaudhry and Sidhu, 2022). *S. domestica* is a fruit-bearing tree in the Rosaceae family, a temperate forest species pollinated by insects (Kamm et al., 2009) and has potential as an urban and landscape greenery plant (Schmucker et al., 2024). This species can adapt to dry, mild climates, which underscoring its relevance in the context of future climate change adaptation. As a forest fruit tree, *S. domestica* coexists with other plant species in forest ecosystems; its fruits serve as a food source for animals and are also valued for their antioxidant properties (Termentzi et al., 2009). Additionally, it can be used to produce high-quality hardwood veneer, serving the timber industry. Habitat loss due to climate change represents a major threat to *S. domestica* (Afifi et al., 2023). Changes in global temperature gradients, altered precipitation patterns, and extreme weather events pose significant threats to its survival. *S. domestica* may respond to these threats through migration, facilitated by its reproductive strategies. This species relies on sexual reproduction and seed dispersal to colonize new, suitable habitats, thereby altering its habitat range (Rasmussen and Kollmann, 2004). Research has shown that *S. domestica* exhibits high molecular and genetic diversity, enabling it to adapt to new habitats through natural selection and increasing the likelihood of successful migration (George et al., 2015). As a mountainous forest species, *S. domestica* is likely to shift to higher altitudes under future climate scenarios. Higher-altitude regions may provide favorable conditions, such as optimal temperature and precipitation levels. Through its migratory capacity, *S. domestica* may establish new habitats in these higher-altitude regions.

Species distribution models (SDMs) are widely employed to predict and interpret the impacts of climate change on species habitat shifts and the contributions of environmental factors (Elith and Leathwick, 2009). In studies on forest tree species, SDMs have been used to predict future habitat distributions under climate change, often revealing reductions in suitable habitats (Iverson and Prasad, 2002). For example, research on larch has not only used SDMs to predict habitat changes but has also provided insights into the relative importance of environmental factors (Leng et al., 2008). Expanding on these applications, studies on tulip trees have combined SDM predictions with analyses of physiological indicators related to stress tolerance (Shen et al., 2022). While these studies have offered valuable insights into species habitat distribution and environmental contributions, they have not thoroughly explored altitudinal habitat shifts driven by climate change. To address this gap, the present study applies SDMs to predict current and future habitat distributions, focusing specifically on altitudinal shifts to uncover trends in species migration under changing climate conditions. SDMs have become indispensable tools for predicting climate change effects on species habitats and play a crucial role in conservation planning and decision-making (Guisan et al., 2013).

Species migrate to new habitats in response to environmental changes. Studies have shown that 84% of species' habitat shifts align with climate change, with migrations typically moving toward higher latitudes and altitudes (Hickling et al., 2006; Thomas, 2010). Research indicates that the median migration distance of species is 11 meters per decade toward higher altitudes and 16.9 kilometers per decade toward higher latitudes (Chen et al., 2011). To adapt to the climate changes of the 21st century,

plant species would need to migrate at rates of 300 to 500 kilometers per century. However, observed migration rates are typically only 20 to 40 kilometers per century, falling well short of this requirement (Chen et al., 2011). Historical and current data have been used to analyze plant migration distances to higher altitudes. For instance, a study of 171 forest tree species in Western Europe during the 20th century found that their most suitable elevation increased by an average of 29 meters per decade (Lenoir et al., 2008). Similarly, research on vascular plants in the Alps revealed a median migration distance of 12.9 meters per decade for 52 species (Lenoir et al., 2008). However, trees often face challenges in migration. Habitat fragmentation and the limited migratory capacity can hinder the speed of tree migration, resulting in habitat contraction or even local extinction.

The impact of climate change on the habitat distribution of *S. domestica* remains uncertain. Therefore, our study aims to (1) analyze the current and future habitat distribution and changes of *S. domestica* under different climate scenarios; (2) identify the key environmental factors influencing its distribution; and (3) investigate the potential trend of its migration to higher altitudes in the future. Predicting the habitat changes of *S. domestica* is essential for mitigating habitat degradation and conserving biodiversity, thereby safeguarding its ecological and economic value in the future.

2. Materials and Methods

2.1 Species occurrence data

The study area encompasses the entire territory of Italy, covering a total area of 302,109.57 square kilometers. Italy is situated between latitudes 36°28'N and 47°6'N, and longitudes 6°38'E and 18°31'E. Records of *S. domestica* occurrences were obtained from the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>) and the Portal to the Flora of Italy (<https://dryades.units.it/floritaly/index.php>). We compiled two datasets (n = 538) and, after screening the data points, removed those with inaccurate geographic coordinates. Subsequently, we used the Spatially Rarefy Occurrence Data tool of SDMtoolbox Pro v0.9.1 in ArcGIS Pro 3.2 to reduce spatial autocorrelation by ensuring that each grid cell contained only one occurrence record, resulting in a final dataset of 239 records.

2.2 Environmental data and contrast experiment

This study utilized 11 environmental variables, including 4 climate variables, 6 landscape variables, and 1 elevation variable, to develop models assessing the habitat distribution of *S. domestica* (Table 1). All data were standardized to the WGS 1984 coordinate system and processed at a spatial resolution of 30 seconds (approximately 1 kilometer). Climate and elevation data were sourced from the WorldClim database (<https://www.worldclim.org/>), while landscape data were derived from the SoilGrids database (<https://soilgrids.org/>), published by the International Soil Reference and Information Center (ISRIC), the Italian Hydrological Network database (Yan et al., 2022), and Land Use and Land Cover (LULC) product data from publicly available databases (REF) (Zhang et al., 2023). National and regional administrative boundaries of Italy (Fig. S1) were provided by the Italian National Institute of Statistics (ISTAT, 2019)

(<https://www.istat.it/>). To ensure that the selection of environmental variables aligns with the ecological adaptability of the species, we selected key climate, landscape, and topographical factors based on habitat characteristics of the study area and known ecological research findings (Paganová, 2007). The climate variables include annual mean temperature (Bio-1), mean temperature of driest quarter (Bio-9), annual precipitation (Bio-12), and precipitation of the driest month (Bio-14). These variables directly reflect climate regulation on the species' requirements for temperature and moisture, which are critical factors in determining the physiological adaptability and distribution patterns of *S. domestica*. The landscape variables include soil organic carbon (SOC), clay content (Clay), pH in the soil (pH), water content (WC), river network distribution (River), and Land Use and Land Cover (LULC). The selection of these landscape variables is based on their significant influence on habitat conditions: SOC and clay content are strongly associated with soil fertility, aeration, and organic matter content, which directly affect nutrient availability and the root environment for plants. Soil pH regulates chemical properties and microbial activity, indirectly influencing nutrient utilization efficiency. WC serves as a key indicator of water availability, which is crucial for plant growth, particularly under drought stress. The spatial distribution of river networks relates to flood risks, soil moisture, and seed dispersal, all of which are essential for species survival and dispersal. LULC shapes habitat structure and community composition, significantly shapes species competition and habitat quality. Elevation, as a topographic factor, determines temperature gradients, precipitation patterns, and light intensity across the study area, thereby influencing ecological adaptability and vertical species distribution range on a large spatial scale. To further investigate the impact of landscape variables on habitat distribution predictions for *S. domestica*, we constructed two models with different combinations of environmental variables. One model, termed "Climate Driven" (CD), included only climate and elevation variables, while the second model, termed "Landscape Climate Driven" (LCD), incorporated landscape variables alongside the base environmental factors. This dual-model approach systematic evaluation the independent contribution of landscape variables to predicting habitat distribution. For future climate scenarios, we adopted the Shared Socio-economic Pathway (SSP) scenarios from the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report (AR6), focusing on an intermediate greenhouse gas (GHG) emissions scenario (SSP2-4.5) and an extremely high GHG emissions scenario (SSP5-8.5). SSP2-4.5 represents moderate mitigation efforts, limiting global temperature rise to approximately 3°C, whereas SSP5-8.5 reflects high economic growth and heavy fossil fuel dependence, leading to an extreme temperature rise exceeding 4°C. To minimize uncertainties associated with a single climate model, we utilized three global climate models (GCMs): CMCC-ESM2, GISS-E2.1, and INM-CM5. The outputs of these models were averaged to derive future climate variables. This ensemble approach improves the reliability and robustness of climate projections, offering a more accurate assessment of the potential impacts of future climate change on species habitat distribution.

Table 1
Descriptions of the 11 types of environmental variables

Variables	Description	Unit
Bio-1	Annual mean temperature	°C*10
Bio-9	Mean temperature of driest quarter	°C*10
Bio-12	Annual precipitation	mm
Bio-14	Precipitation of driest month	mm
Elevation	Vertical height from mean sea level	m
SOC	Soil organic carbon	dg/kg
Clay	Clay content	g/kg
pH	pH in the soil	/
WC	Water content at -10 kPa	$(10^{-2} \text{cm}^3 \text{cm}^{-3}) \times 10$
River	River network distribution	/
LULC	Land use and land cover: cropland, forest, grassland, urban, barren, and water	/

2.3 Species distribution modeling and evaluation

In this study, we utilized the "biomod2"(version 4.2.4) package in R 4.3.2, to develop species distribution models (SDMs). Two sets of pseudo-absences, each containing 5,000 points, were randomly generated (Fig. S1). For single-model development, we employed the following algorithms: Artificial Neural Networks (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Models (GAM), Gradient Boosting Machine (GBM), Generalized Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS), Maximum Entropy (MaxEnt), Random Forest (RF), Surface Range Envelope (SRE), and eXtreme Gradient Boosting (XGBOOST). We selected a subset of these single models with AUC values exceeding 0.8 to construct an ensemble model. Model performance was evaluated using random ten-fold cross-validation, with 80% of the data allocated to the training set and 20% to the test set for each fold. The performance metrics for both single models and the ensemble model included the Area Under Curve (AUC), True Skill Statistic (TSS), Sensitivity, and Specificity. Additionally, we calculated the contribution of environmental variables within the ensemble model. To quantify species habitat, we converted predicted habitat distribution probabilities (i.e., species habitat suitability) into binary classifications of "presence" and "absence" using a probability threshold of 0.6. The suitable habitat area was then calculated to compare habitat changes across different climate scenarios. Additionally, using Italy's administrative divisions, we quantified the area occupied by suitable habitats within each region. To compare current and future habitat distributions, we used SDMtoolbox Pro (v0.9.1), calculating the Gain, Loss, and Stable areas of suitable habitats. Elevation data for future

climate scenarios were analyzed to study trends in the migration of *S. domestica* to higher altitudes. By recording the latitude and longitude from the current and future habitat distributions of *S. domestica*, we extracted the corresponding elevation variables. The maximum, minimum, average, and median elevation values of current and future habitats were calculated to assess changes in the elevation of *S. domestica* habitats under future climate scenarios.

3. Results

3.1 Modeling results validation

By comparing the evaluation results of the single models and ensemble models (Table 2, Table 3). We found that the ensemble model performed the best. In the model developed for LCD approach, the ensemble model achieved an AUC of 0.87, significantly exceeding the average AUC of the individual models (0.83). Additionally, the ensemble model's TSS reached 0.63, higher than that of any single model (Table 2). In the model based on CD, the ensemble model achieved an AUC of 0.85, outperforming the average AUC of the 11 individual models (0.82). The ensemble model for CD also recorded the highest TSS value of 0.65 (Table 3). Based on these comparisons, the ensemble model was selected as the most effective tool for predicting habitat distribution. The ensemble model for LCD showed a slightly higher AUC value (0.87) compared to the CD model (0.62). Additionally, the ensemble model for LCD also showed a slightly higher TSS value (0.63) compared to the CD model (0.62).

Table 2

Model performance of 11 individual models and the ensemble model built using LCD. The table records the mean and standard deviation (denoted by $\pm$) of AUC, TSS, Sensitivity, and Specificity for each model.

Model	AUC	TSS	Sensitivity	Specificity
ANN	0.81 ± 0.03	0.48 ± 0.07	79.23 ± 5.62	78.74 ± 4.26
CTA	0.81 ± 0.04	0.55 ± 0.07	87.48 ± 6.97	82.38 ± 2.56
FDA	0.85 ± 0.03	0.55 ± 0.06	84.29 ± 4.45	74.10 ± 3.70
GAM	0.83 ± 0.03	0.56 ± 0.04	78.79 ± 2.73	79.80 ± 2.76
GBM	0.88 ± 0.02	0.60 ± 0.05	89.03 ± 1.82	84.50 ± 1.86
GLM	0.85 ± 0.02	0.58 ± 0.05	84.10 ± 2.71	77.27 ± 2.65
MARS	0.87 ± 0.02	0.59 ± 0.05	86.39 ± 2.91	77.28 ± 2.75
MAXENT	0.88 ± 0.02	0.59 ± 0.06	85.10 ± 2.71	81.10 ± 2.83
RF	0.88 ± 0.02	0.31 ± 0.11	100.00 ± 0.00	99.56 ± 0.19
SRE	0.69 ± 0.03	0.39 ± 0.05	76.03 ± 1.05	65.41 ± 1.33
XGBOOST	0.83 ± 0.02	0.54 ± 0.06	85.85 ± 5.11	75.89 ± 3.82
Ensemble	0.87 ± 0.02	0.63 ± 0.04	88.74 ± 1.84	82.16 ± 1.95

Table 3

Model performance of 11 individual models and the ensemble model built using CD. The table records the mean and standard deviation (denoted by $\pm$) of AUC, TSS, Sensitivity, and Specificity for each model.

Model	AUC	TSS	Sensitivity	Specificity
ANN	0.84 $\pm$ 0.03	0.58 $\pm$ 0.07	85.03 $\pm$ 3.88	73.11 $\pm$ 14.98
CTA	0.80 $\pm$ 0.04	0.57 $\pm$ 0.05	86.17 $\pm$ 4.07	80.54 $\pm$ 3.86
FDA	0.83 $\pm$ 0.03	0.55 $\pm$ 0.05	79.10 $\pm$ 3.59	77.30 $\pm$ 3.85
GAM	0.82 $\pm$ 0.02	0.55 $\pm$ 0.05	79.99 $\pm$ 2.39	74.67 $\pm$ 1.81
GBM	0.87 $\pm$ 0.02	0.60 $\pm$ 0.05	88.96 $\pm$ 1.98	80.56 $\pm$ 2.31
GLM	0.83 $\pm$ 0.02	0.53 $\pm$ 0.06	84.41 $\pm$ 2.45	69.47 $\pm$ 2.23
MARS	0.84 $\pm$ 0.02	0.53 $\pm$ 0.05	80.24 $\pm$ 4.29	77.66 $\pm$ 4.10
MAXENT	0.85 $\pm$ 0.02	0.55 $\pm$ 0.04	78.97 $\pm$ 2.63	79.49 $\pm$ 2.22
RF	0.87 $\pm$ 0.02	0.24 $\pm$ 0.05	99.97 $\pm$ 0.13	99.60 $\pm$ 0.18
SRE	0.69 $\pm$ 0.03	0.37 $\pm$ 0.05	82.58 $\pm$ 0.65	58.67 $\pm$ 2.27
XGOOST	0.82 $\pm$ 0.03	0.54 $\pm$ 0.06	85.12 $\pm$ 4.23	74.27 $\pm$ 6.05
Ensemble	0.85 $\pm$ 0.02	0.62 $\pm$ 0.06	85.54 $\pm$ 2.17	85.22 $\pm$ 4.51

3.2 Current and future habitat distribution

The habitat prediction results under current climate conditions (Fig. 1a) indicate that the primary suitable habitat areas for *S. domestica* are concentrated in the Apennine Mountains, particularly within the central Italian regions of Toscana and Emilia-Romagna (Fig. S1). Toscana contains the largest distribution of *S. domestica* habitats, covering approximately 12,399.21 square kilometers, accounting for 48% of the total habitat area (Table S1). In Emilia-Romagna, the habitat area comprises about 11% of the total. In Liguria, suitable habitats are mainly distributed along the coastal side. In southern Italy, suitable habitats are mainly found in Lazio and Campania, collectively accounting for approximately 11% of the overall habitat area. Future climate scenarios predict a significant reduction in suitable habitat areas for *S. domestica* compared to current conditions (Fig. 1). Under SSP5-8.5, habitat loss is notably more severe than under SSP2-4.5 (Fig. 1c, e). Under extreme climate conditions (SSP5-8.5), *S. domestica* is expected to experience widespread habitat loss. By 2050, the habitat area projected to decrease by 3,040.11 square kilometers under SSP5-8.5. By 2100, the loss will reach 5,162.83 square kilometers, representing 20% of the current habitat area (Table S2).

3.3 Future changes in Suitable habitat distribution

We compared the current and future habitat distributions of *S. domestica* (Fig. 2). Habitat loss is primarily concentrated in the Toscana region (Fig. S1), where approximately 40% of the total habitat loss under 2050 SSP5-8.5 2050 and 2100 SSP5-8.5 (Table S3). Significant habitat loss is also observed in the northern parts of Emilia-Romagna and Liguria. By 2050, under SSP2-4.5, a substantial portion of Emilia-Romagna's habitat will significantly decrease, with even more pronounced losses under SSP5-8.5 for 2050 and 2100, as well as in SSP5-8.5 for 2100. When comparing current and future climate conditions, habitats in regions such as Campania, Marche, Basilicata, Molise, Abruzzo, Puglia, Sardegna, and Sicilia are expected to disappear entirely. In Umbria, about half of the habitat is projected to vanish by 2050 under SSP2-4.5. By 2050 (SSP5-8.5) and 2100 (SSP5-8.5), all habitats in Umbria are expected to disappear. In the future, habitat loss in Lazio and Umbria will account for approximately half of the total loss, with the most severe declines occurring under SSP5-8.5 in 2100. Overall, *S. domestica* habitats are predicted to decrease significantly under future climate conditions, with the greatest losses under SSP5-8.5 compared to SSP2-4.5. However, regions like Toscana, Emilia-Romagna, and Liguria are expected to retain more habitats, suggesting that these areas will remain the primary distribution zones for the species. In Toscana, while habitats are projected to decrease overall, some areas, particularly in the eastern part of the region, may experience slight increases. The increase in suitable habitats across Italy is mainly concentrated in the southern regions of Lazio and Calabria. In Lazio, the habitat increase in 2100 under SSP5-8.5 is smaller compared to the 2050 SSP2-4.5, 2050 SSP5-8.5, and 2100 SSP2-4.5 scenarios. In Calabria, new habitat areas are expected to appear in a banded pattern, with greater increases under SSP5-8.5 than under SSP2-4.5.

3.4 Feature contribution and functional response

Based on the model's calculation of feature contributions, the four variables with the highest contributions are Bio-9, Elevation, SOC, and Bio-1 (Fig. 3). Bio-9 has the greatest influence on species prediction, followed by Elevation, SOC, and Bio-1. Among these high-contributing variables, the contributions of Elevation, SOC, and Bio-1 are relatively similar. Soil variables contribute more to the model than land cover and hydrological variables, which have the lowest contributions in the evaluation. Among the soil variables, SOC has a higher contribution than other soil variables. Our results indicate that as the mean temperature of the driest quarter (Bio-9) increases, the probability of habitat suitability also rises. The probability of habitat suitability peaks at 22°C, representing a 'tipping point' for the species' survival (Fig. 3b). If the mean temperature of driest quarter continues to rise above 22°C, it will pose a significant threat to the survival of the species. The response curve for Elevation reveals that the most suitable elevation range for *S. domestica* is 0–500 meters. As elevation increases, the species' survival probability gradually decreases, reaching its lowest distribution probability (approximately 10%) at 1000 meters. Above 1000 meters, the species' survival probability increases again. Regarding SOC content, when levels are below 250 dg/kg, the species' survival probability gradually declines. The species' lowest habitat suitability occurs at around 250 dg/kg SOC content. However, once SOC content exceeds 250 dg/kg, the survival probability increases as SOC levels rise. For the annual average temperature (Bio-1), the species' survival probability remains stable below 10°C but decreases gradually when temperatures exceed 10°C.

3.5 Future Habitat Shift

We recorded the elevation data of suitable habitats for the species under current and four future climate scenarios (Fig. 4). The results reveal a clear trend of migration to higher elevations under future climate conditions. Under the extreme climate conditions of the 2100 SSP5-8.5, the species' average habitat elevation increases by approximately 160 meters compared to other climate scenarios (Table S4). Under current climate conditions, 2050 SSP2-4.5 and 2100 SSP2-4.5, the highest elevations for suitable habitats are 1,022 meters, 987 meters, and 890 meters, respectively. In contrast, under 2050 SSP5-8.5 and 2100 SSP5-8.5, the highest elevations for suitable habitats rise to 1,106 meters and 1,105 meters, approximately 100 meters higher than those under current climate conditions and the SSP2-4.5 scenarios. Additionally, under 2100 SSP5-8.5, the species' lowest habitat elevation increases to 78 meters, which is over 70 meters higher than in other climate scenarios.

4. Discussion

S. domestica is primarily distributed in the mountainous regions of central Italy. This species is significant for both urban and forest environments and demonstrates potential adaptability to climate change. However, research on the impact of climate change on the habitat distribution of *S. domestica* remains limited. Our habitat prediction results indicate that the most suitable areas for *S. domestica* are located in the Apennine Mountains on the edge of Tuscany in central Italy, as well as the coastal mountains of Liguria. Under future climate change scenarios, *S. domestica* habitats are projected to gradually diminish, with the remaining suitable habitats primarily concentrated in the Apennine Mountains (Fig. 2). The study also identifies the average temperature during the driest months (Bio-9) as the most significant factor influencing the survival of this species. Statistical analysis of the elevation data reveals a trend of migration to higher altitudes under future climate conditions, particularly under the 2100 SSP5-8.5 scenario, where this upward migration is most pronounced.

4.1 Future habitat shift to higher elevations

Global warming has become an irreversible phenomenon, profoundly impacting plant habitat distribution. Our results findings indicate that the primary habitats of *S. domestica* are concentrated in mountainous regions. However, as GHG emissions intensify, its habitat area is projected to shrink progressively (Fig. 1). The principal areas of habitat reduction are concentrated on both sides of the Apennine Mountains, and under the 2100 SSP5-8.5 scenario, most of the habitat in the study area is projected to disappear, with significant reductions occurring in the Apennines' core areas. This result aligns with our expectations that climate change is altering the species' living conditions and that the migration rate of *S. domestica* cannot keep pace with the rapid shifts in climate, leading to a continued contraction of its habitat. The loss of habitat not only threatens the species itself but also raises ecological concerns, including declines in biodiversity, diminished food supply, and reduced carbon storage capacity in ecosystems (Brockhoff et al., 2017). Unlike other regions, however, the Lazio region in central Italy may experience an increase in habitat under future climate scenarios. The newly formed

habitats are located in the low-lying areas between the northern and southern mountain ranges. This topography traps cold air in the valleys during winter, hindering the growth of *S. domestica* seedlings. Rising temperatures due to global warming may make these areas more suitable, facilitating the establishment of new habitats. Under the SSP5-8.5 scenario for 2100, the extent of newly formed habitats in Lazio is projected to be smaller compared to SSP2-4.5. While the terrain's winter cooling effect may offer some protection, further warming could exceed the species' thermal tolerance, thereby limiting habitat expansion. Furthermore, our analysis reveals that the Calabria region in southern Italy, currently almost devoid of *S. domestica* habitats, may develop new habitats in Calabria. These habitats are expected to exhibit a linear distribution, predominantly in mountainous areas. The gradient variations in temperature and precipitation with elevation create conditions conducive to the ecological requirements of *S. domestica*, enabling the formation of linear, coherent habitats at suitable altitudes.

4.2 Feature contribution and functional response

Although *S. domestica* exhibits certain heat and drought tolerance traits, our results reveal that the average temperature of the driest months is the most influential factor in predicting habitat suitability (Fig. 3). This finding aligns with previous research, which reported that *S. domestica* demonstrates relatively low resistance to extreme drought and high-temperature events, significantly impacting its growth rate (Kunz et al., 2018). The threats posed by drought and elevated temperatures to *S. domestica* are primarily manifested in several ways: when temperatures exceed its upper tolerance limit, physiological disruptions occur, including reduced enzyme activity, stomatal closure leading to diminished photosynthetic efficiency and dehydration due to water stress. Our study indicates that when the mean temperature of the driest quarter reaches 22°C, the probability of habitat suitability for the species declines markedly, suggesting that 22°C represents a critical threshold for its tolerance. While the species can recover radial growth after extreme climatic events, the ongoing and irreversible nature of global climate change will continue to alter its suitable habitat, posing a long-term threat to its survival.

By comparing the predictions of the CD and LCD models, we identified significant differences in the predicted habitat distribution of *S. domestica* in the southern Apennine Mountains of central Tuscany, Italy. Previous studies have documented *S. domestica* within vascular plant communities in this region (Da Vela et al., 2013). In our study, predictions based on the multivariate environmental model demonstrated higher accuracy compared to those derived from the basic climate model. The LCD model, which incorporated additional variables such as soil, hydrology, and land cover, significantly improved the accuracy of habitat distribution predictions for *S. domestica* (Fig. 3). Consequently, we recommend that future research include a broader range of environmental variables to enhance the precision of habitat suitability models.

4.3 Future habitat shift to higher altitudes

Through statistical analysis of habitat elevation distribution under various climate scenarios, we observed a clear trend of *S. domestica* migrating to higher altitudes in response to climate change.

Specifically, the highest elevation of its habitat was recorded at approximately 1,100 meters, with habitat distribution under the SSP5-8.5 scenario being about 100 meters higher than under SSP2-4.5 (Fig. 4). By 2100, the trend of habitat migration to higher altitudes is expected to be particularly pronounced under the SSP5-8.5 scenario, with the average elevation of *S. domestica* habitats rising by roughly 160 meters compared to other scenarios (current climate, 2050 SSP2-4.5, 2050 SSP5-8.5, and 2100 SSP2-4.5). This study identified 1,100 meters as the upper elevation limit for the species' survival under the most severe greenhouse gas (GHG) emissions scenario (SSP5-8.5). Beyond this altitude, factors such as lower temperatures, reduced precipitation, and altered soil composition are projected to hinder its survival. Climate change has rendered conditions at lower altitudes unsuitable for *S. domestica*, compelling the species to migrate to higher elevations in search of suitable habitats. Higher altitudes may offer more favorable temperature and light conditions; however, this migration is not without limits. The strong winds in higher altitude areas, along with the increased risk of organic carbon loss and permafrost in the central Apennines due to low clay content and steep slopes, are unfavorable for the growth of *S. domestica* seedlings (Tomaselli et al., 2019; Vittori Antisari et al., 2022). By 2100 under the SSP5-8.5 scenario, the species' lowest habitat elevation is projected to rise to about 78 meters, leaving areas below this altitude incapable of supporting its survival, potentially leading to habitat fragmentation or even extinction. These findings underscore the extent of *S. domestica*'s upward migration due to climate change (Fig. 4). However, this migration may trigger a range of ecological consequences. First, the arrival of *S. domestica* at higher altitudes could alter the composition of existing microbial, plant, and animal communities, disrupting local ecological balances. Moreover, as a newly established species, it may introduce pathogens that pose threats to native species with slower migration rates (Alexander et al., 2015; Pauchard et al., 2016). Additionally, as a new competitor, *S. domestica* may compete with existing species for space and resources, potentially reshaping the structure and functions of local ecosystems. The upward migration of *S. domestica* due to future climate warming, along with its associated ecological impacts, offers critical insights for conserving the species' habitats while maintaining ecological balance.

5. Conclusion

In this study, we present the first application of Species Distribution Models (SDMs) to predict changes in the habitat distribution of *Sorbus domestica* L. under current and future climate scenarios. Our analysis reveals the environmental factors influencing its distribution and highlights the role of landscape variables in improving habitat prediction accuracy. Notably, we identified a trend of *S. domestica* migrating to higher altitudes in response to climate change. When predicting the current habitat distribution, we compared two models with different environmental factor inputs and found that incorporating landscape variables significantly enhances prediction accuracy. These findings provide valuable insights for future SDM-based studies on habitat prediction for forest tree species. Our results indicate that the primary habitat of *S. domestica* is concentrated in central Italy. Under future climate scenarios, its habitat is projected to decline substantially, with a risk of complete habitat loss in certain regions. Feature importance analysis identified the average temperature of the driest months as the

most significant factor influencing habitat distribution. Additionally, under future climate scenarios, *S. domestica* shows a clear trend of migrating to higher altitudes. These findings offer critical insights into the conservation and management of *S. domestica*, which are vital for protecting rare species and preserving biodiversity. Such conservation efforts will help ensure that *S. domestica* continues to provide ecosystem services and maintain its ecological value in the future. Furthermore, this study provides a methodological framework for investigating altitudinal shifts in other forest tree species, supporting broader research efforts to understand the impacts of climate change on species survival.

Declarations

Acknowledgments

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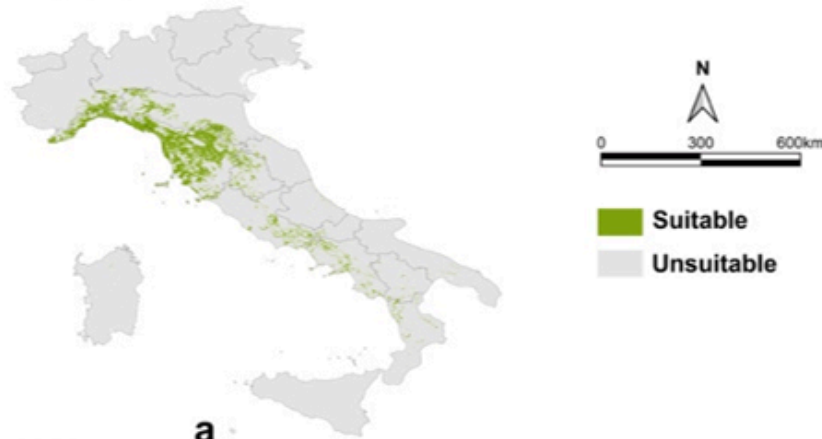
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Figures

Present



**2050
ssp245**

a

ssp585

**2100
ssp245**

b

ssp585

c

d

e

Figure 1

Distribution of *S. domestica* habitat under current climate conditions and future climate scenarios (2050-SSP2-4.5, 2050-SSP5-8.5, 2100-SSP2-4.5, and 2100-SSP5-8.5). Green is suitable habitat distribution, while grey indicates areas where habitat is not suitable.

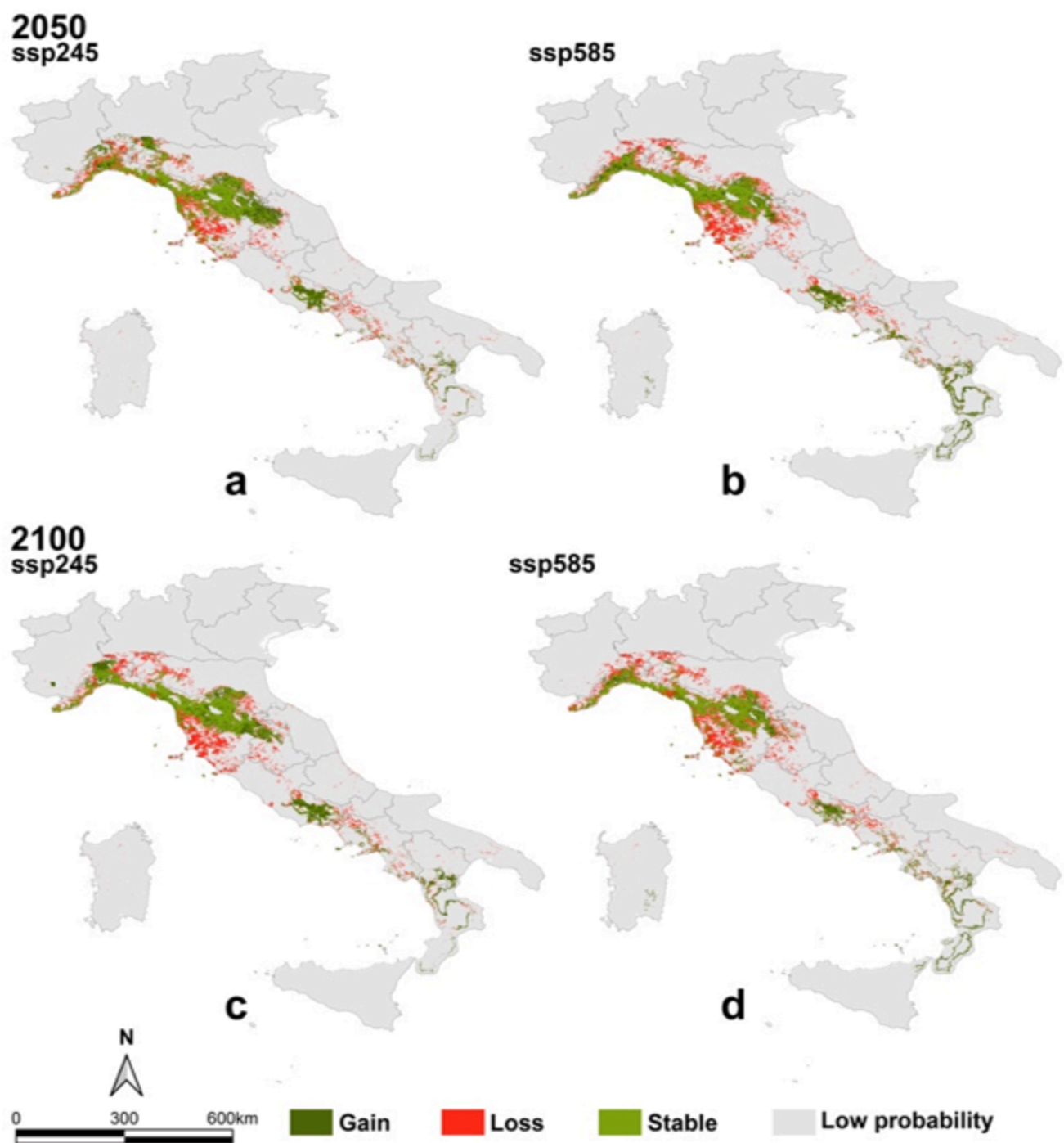


Figure 2

Comparison of the distribution of *S. domestica* habitats under current climate conditions and future climate scenarios (2050-SSP2-4.5, 2050-SSP5-8.5, 2100-SSP2-4.5, and 2100-SSP5-8.5). Dark green is newly gained habitats, red represents habitat loss, green represents unchanged habitats, and gray represents areas where habitat is not suitable.

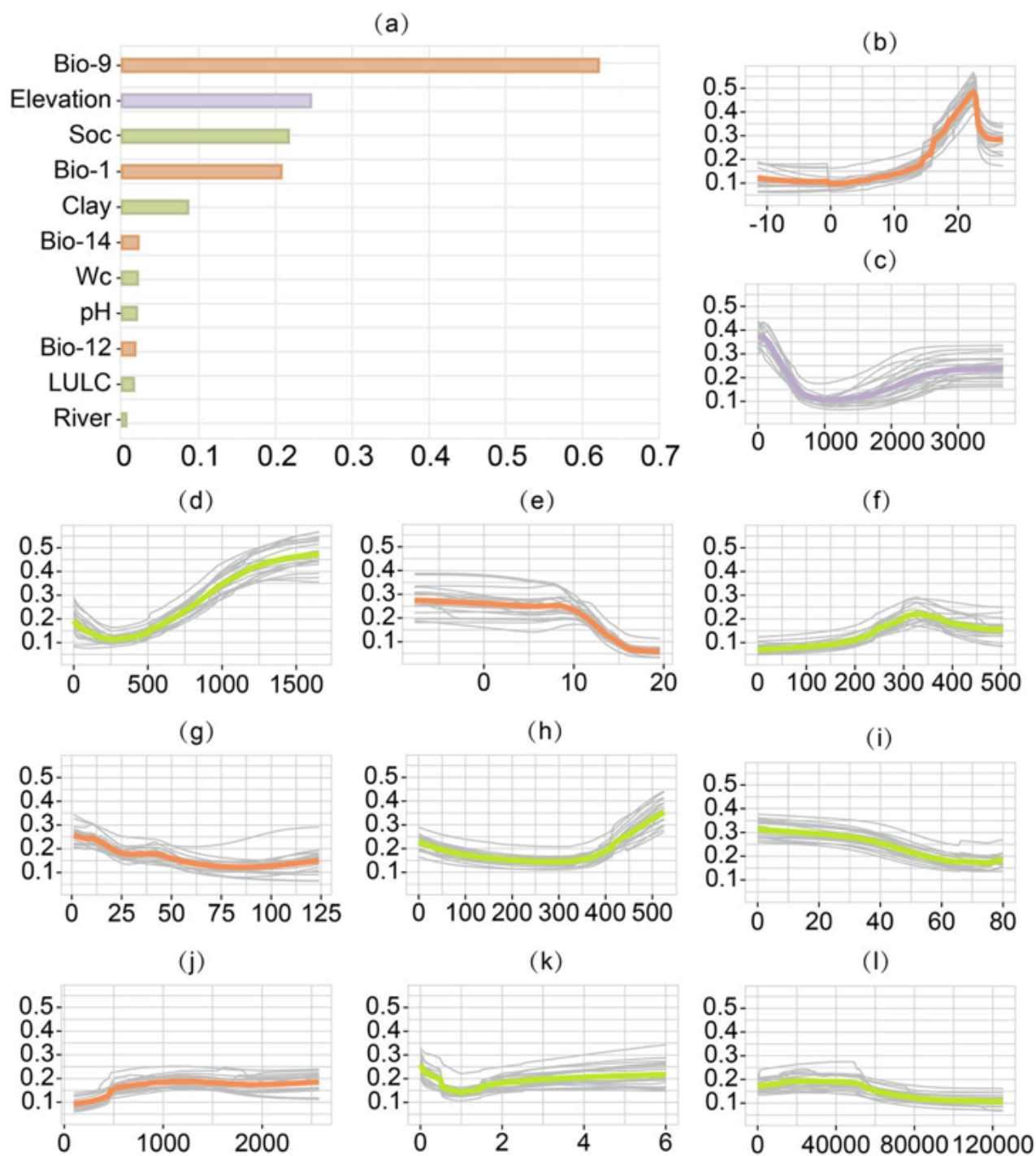


Figure 3

Ranking of environmental variable contributions (a) and response curves (b-l). The ranking of environmental variable contributions (a) shows the relative importance of each environmental variable in influencing habitat prediction. The response curves (b-l) illustrate the relationship between each environmental variable and the species' survival probability. The order of the response curves (b-l)

corresponds to the importance ranking of environmental variables (a). Orange is climate variables, green represents landscape variables, and purple represents elevation variables.

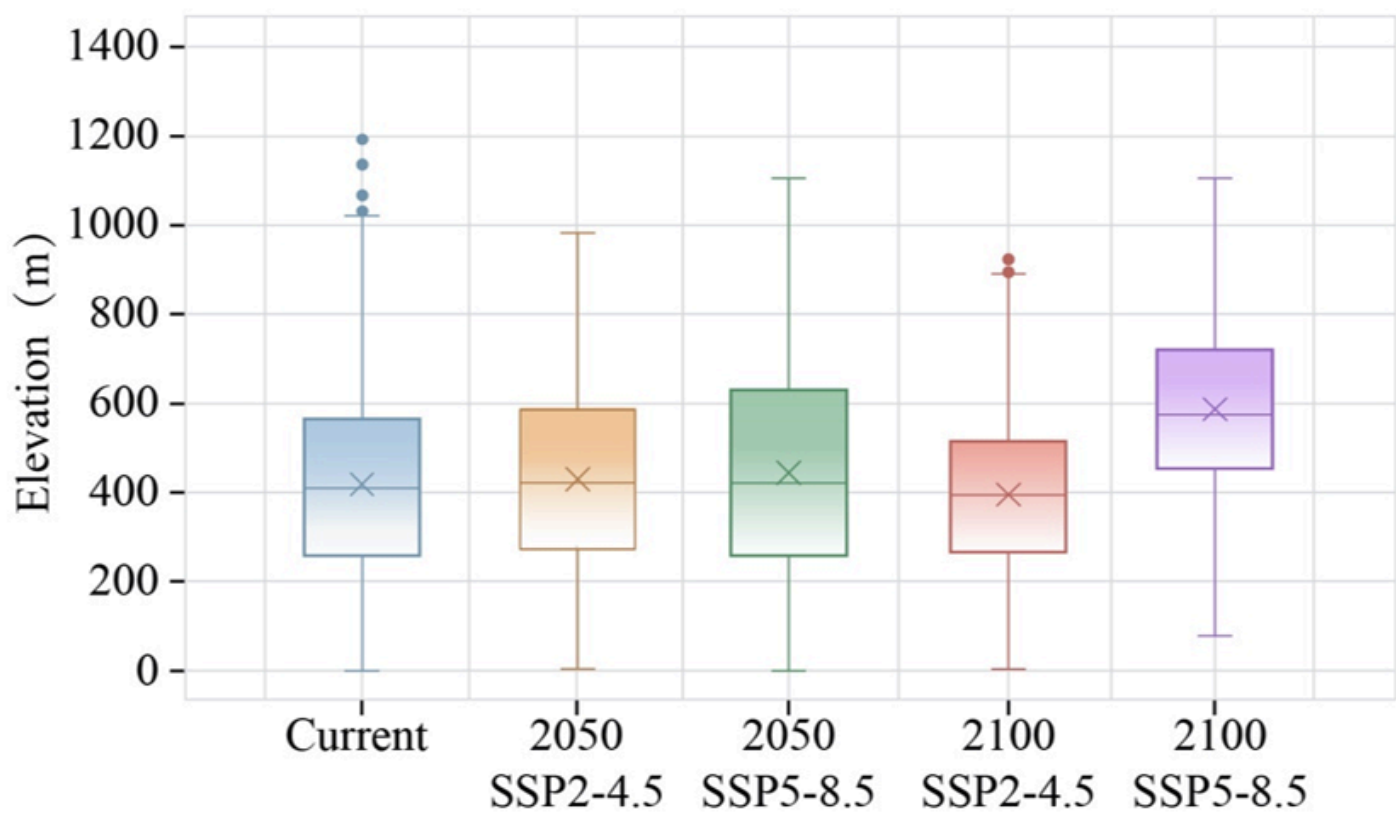


Figure 4

Elevation data statistics of suitable habitats. The squares are the middle 50% of the elevation data for habitat distribution under different climate scenarios, with the horizontal line in the center showing the median. The cross marks are the mean value. The top and bottom horizontal lines are the maximum and minimum values, respectively. The dots are outliers.