Geographic Range Shifts of Taiwan's Endemic Plant Species *Prunus transarisanensis* under Climate Change

氣候變遷下臺灣特有植物阿里山櫻花 (*Prunus transarisanensis*) 的地理分布變化

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Abstract

Climate change is driving shifts in the species distribution, and its impact is particularly pronounced on high mountain plants sensitive to warming. *Prunus transarisanensis* is an endemic species found exclusively in the high-altitude regions of Taiwan, known for its ornamental cherry tree. In this study, species survey records and environmental data were integrated, and ensemble ecological niche modeling was employed to predict the current and future suitable habitats, as well as their spatiotemporal dynamics for *P. transarisanensis* under various climate scenarios (shared socioeconomic pathways SSP126, SSP370, SSP585, 2071-2100). The model identified that a cool environment and moderate precipitation are key characteristics for suitable habitats of *P. transarisanensis*. In the analysis of the dynamics of suitable habitat distribution under three future scenarios, it was found that climate change will transform a significant portion of the currently suitable habitats into vulnerable states, regardless of the scenario. Even under the low emission scenario (SSP126), only a small portion of suitable habitat may persist as refugia. However, under the SSP370 or SSP585 scenarios, habitat degradation will be more severe, potentially leading to a high risk of extinction for the species. Based on the above results, this study proposes several suggestions to assist *P. transarisanensis* to adapt to climate change.

Key words: range dynamics, ensemble ecological niche modeling, shared socioeconomic pathways, extinction, conservation

摘要

氣候變遷正在驅使生物的地理分布發生改變，對暖化敏感的高山植物而言，其影響尤為顯著。阿里山櫻花 (*Prunus transarisanensis*) 分布於臺灣高海拔地區，是一種具觀賞價值的特有種櫻花。本研究整合物種調查及環境資料，運用集成生態棲位建模，預測當前和未來氣候情境 (共享社會經濟路徑 SSP126、SSP370、SSP585，2071-2100 年) 下，該物種之適宜生育地範圍及其時空分布動態。由所建構的集成模型可發現，冷涼環境與適度降水，是阿里山櫻花適宜生育地的關鍵特徵。未來 3 種情境下的適宜生育地分布動態分析結果顯示，無論何種情境，氣候變遷都將導致當前適宜生育地，大幅轉為脆弱狀態，即便是低碳排的 SSP126 情境下，也僅能保存少部分適宜生育地，供作避難所，而在 SSP370 或 SSP585

情境下，生育地退化情況將更顯嚴峻，最終可能導致該物種面臨高度滅絕風險。綜合上述推測結果，本研究最後也提出了幾點協助阿里山櫻花調適氣候變遷的建議。

關鍵詞：分布動態、集成生態棲位建模、共享社會經濟路徑、滅絕、保育

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Introduction

Climate change has been regarded as an unavoidable global phenomenon of this century and the most significant threat to Earth's biodiversity (Warren *et al.* 2013; Urban 2015). Within the next 50 years, approximately one-third of the world's species may face the threat of extinction due to this phenomenon (Román-Palacios and Wiens 2020). The complex terrain of high mountains fosters species diversity and endemism (Steinbauer *et al.* 2016; Noroozi *et al.* 2018). However, due to isolation effects, it also shapes the rarity, scattered distribution, and narrow habitat range of mountain species. These mountain species are often more sensitive to climate change, especially plant communities (Thuiller *et al.* 2005; Adhikari *et al.* 2018). To adapt to the impacts of climate change, most mountain plant species are shifting towards higher altitudes, tracking new suitable climate zones (Jump *et al.* 2012; Kellner *et al.* 2023). This migration allows them to thrive in environments with optimal conditions for their growth and survival. Unfortunately, under the impact of global warming, as elevation increases, not only does the temperature rise rapidly (Pepin *et al.* 2015; Lamprecht *et al.* 2018), but available areas also are significantly decreasing (Freeman *et al.* 2018). Furthermore, the natural barriers of high mountains restrict the dispersal of plants (Essl *et al.* 2011; Di Musciano *et al.* 2020; Chen *et al.* 2023), exacerbating the impact of climate change on mountain vegetation simultaneously.

Ecological niche modeling (ENM) predicts potential distribution ranges based on the correlation between species presence records and environmental variables. When combined with data on climate change scenarios, it enhances understanding of species responses to climate change and aids in the formulation of conservation strategies (Dhyani *et al.* 2021; Hoveka *et al.* 2022; Ceccarelli *et al.* 2022). ENM has developed various types of algorithms, such as general linear model (GLM) and multivariate adaptive regression splines (MARS) for regression methods, as well as machine learning methods like boosted regression tree (BRT), maximum entropy (MaxEnt), and support vector machine (SVM). Recently, the "ensemble" ecological niche modeling (EENM), which integrates predictions from multiple models, has been continuously evolving. Compared to single models, EENM achieves consensus from multiple algorithms, mitigating the uncertainties in single-model predictions and leading to improved prediction accuracy (Araújo and New 2007; Marmion *et al.* 2009).

Taiwan has many high mountains, and is characterized by complex terrain and environments that have fostered rich and unique plant diversity. Statistical data from the past century indicates that Taiwan has experienced a temperature increase of approximately 1.4°C, which is significantly higher than the global average (Lu *et al.* 2012). Moreover, the rate of warming in high mountain areas has surpassed that of plains and lowlands

(Lin *et al.* 2015). Past studies have examined the effects of climate change on mountain vegetation composition and distribution. For example, Chou *et al.* (2011) predicted that future climate warming would drive changes in Taiwan's mountainous vegetation distribution, causing many plant species to migrate to higher altitudes. Jump *et al.* (2012) observed that the rise of the forest line is consistent with the warming trend. Kuo *et al.* (2022) suggested that some vulnerable species might face the threat of extinction due to climate change.

Prunus transarisanensis is an endemic species of Taiwan, taxonomically classified in the Rosaceae family and the *Prunus* genus. It is found at an elevation of approximately 2,500 m. Its appearance is that of a small shrub tree with whitish or light pink petals (Hsieh and Ohashi 1993). Due to its highly attractive appearance, this tree species is one of the important components of cherry blossom tourism in Taiwan, significantly contributing to the income of the Alishan region each year (Liu *et al.* 2021). However, among various cherry tree species, the habitats of *P. transarisanensis* are situated at relatively higher altitudes, making them susceptible to the impacts of climate change. Consequently, this study assesses future threats to *P. transarisanensis* based on species survey data and EENM. The investigation seeks to determine: (1) what are the major factors affecting species distribution; (2) how the suitable habitat transforms under different climate change scenarios; and (3) if it is highly vulnerable to the impacts of climate change, how can we assist this species in adapting?

Materials and methods

Scope of study and species occurrence record

The geographical area covered by this study is the subtropical island of Taiwan, which has a land area of approximately 36,000 km^2. Its land is predominantly covered by forests, while urban and agricultural areas are mainly located in coastal plains. The island's terrain fluctuates greatly, consisting mostly of mountains and hills. The variation in altitude among the high mountains results in a range of complex climate types, including tropical, subtropical, temperate, and cold zones. Due to this diverse climate, a rich variety of vegetation ecosystems has formed, leading to the identification of 12 types of zonal forests and 9 types of azonal forests (Li *et al.* 2013).

The species occurrence records are derived from the ecological survey database (ecollect.forest.gov.tw). This dataset was systematically collected through island-wide surveys commissioned by the Forestry and Nature Conservation Agency (FANCA), with the collaboration of experts and scholars from various universities and research institutions. Only occurrence records of the genus *Prunus*, totaling 13,301 records and including 86 records of the target species, from the years 1981 to 2010 were extracted to match the time interval of predictors. To maintain precise geographic coordinates, data with fewer than three decimal places were removed. Furthermore, spatial thinning was performed using the "spThin" package in the R version 4.1.3 environment (Aiello-Lammens *et al.* 2015) to reduce the impact of spatial autocorrelation and geographic sampling bias. In order to achieve the spatial resolution required for predictors, a minimum neighbor distance of at least 1 km was set between each occurrence record. After processing, there were 32 occurrence records of *P. transarisanensis* (Fig. 1a), along with 1,230 records of other species.

Environment variables

Climate, soil, and topography are commonly considered factors in assessing the habitat suitability of plant species (Titeux *et al.* 2016; Hageer *et al.* 2017; Wan *et al.* 2019). Therefore, the predictors used encompass these three factors. This study did not incorporate land cover variables because all occurrence records of *P. transarisanensis* were located within forested areas according to the Ministry of the Interior's land use survey results (maps.nlsc.gov.tw). For the current climate scenario, 19 bioclimatic variables (BIO1-BIO19, Table S1) were extracted from the CHELSA V2.1 (chelsa-climate.org), with data spanning from 1981 to 2010 (Karger *et al.* 2017). Soil data were downloaded from the ISRIC-World Soil Information (isric.org) and included six soil variables: coarse fragments volumetric, soil texture fraction clay, soil texture fraction sand, soil texture fraction silt, soil pH, and cation exchange capacity. The digital elevation model was obtained from the Ministry of the Interior (data.gov.tw) and processed using the Surface Tool in ArcGIS 10.8 (ESRI Inc.) software to generate variables such as slope and aspect. The spatial resolution of all layers was re-sampled to 1 × 1 km. To avoid collinearity, a selection was conducted according to Pearson correlation coefficients (< 0.7, Dormann *et al.* 2013). When two variables were highly correlated, the variable with the greatest ecological relevance to *P. transarisanensis* was chosen. The Pearson correlation analysis for environmental variables was performed using the R package "virtualspecies" (Leroy *et al.* 2016).

For future scenarios, CHELSA V2.1 also provides future climate data. Five global circulation models (GCMs, namely GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL) and three greenhouse gas emission scenarios (SSP126, SSP370, and SSP585) were utilized. Each scenario represents radiative forcing increasing by 2.6, 7.0, and 8.5 Wm^{-2} between 1750 and 2100, respectively. The bioclimatic data under these three scenarios for the 2071-2100 period was downloaded. Table S1 shows the mean values within the study area. The future bioclimatic variables generated by each of these five GCMs were used to construct models for *P. transarisanensis*, and the average probability was calculated as the final result to evaluate habitat suitability. Moreover, due to the relative stability of soil and topographical factors, it is assumed that the relevant variables remain constant.

Ensemble ecological niche modeling

The R package "sdm" (Naimi and Araújo 2016) was used to execute EENM to predict a suitable habitat for *P. transarisanensis*. Five algorithms were applied, including BRT, GLM, MARS, MaxEnt, and SVM. Since all algorithms required background data (pseudo-absence points), pseudo-absences could only be selected from areas where other plant species had been recorded, a more objective approach to avoid considering under-sampled areas as unsuitable for *P. transarisanensis* (Ghisbain *et al.* 2020; Lu and Huang 2023). From the occurrence records of *P. transarisanensis*, 70% were randomly selected for the training dataset, while the remaining 30% were allocated to the testing dataset. The model performance of each algorithm was evaluated using bootstrap sampling on the training dataset. The 100 replicates were constructed using five algorithms, resulting in 500 models.

Model accuracy was evaluated using two metrics a threshold-independent statistic—the area under the receiver operating characteristic curve (AUC) (Fielding and Bell 1997) and a threshold-dependent statistic—the true skills statistic (TSS) (Allouche *et al.* 2006). The AUC was produced using the true positive rate (i.e., sensitivity) and the false positive rate from the classification table. The TSS was determined using the sensitivity and the true negative rate (i.e., specificity). Higher values for these two metrics indicate better prediction accuracy of the model. The standard for excellent models was set as values of AUC and TSS higher than 0.9 and 0.8, respectively (González-Ferreras *et al.* 2016). The ensemble method was performed by retaining models with high predictive accuracy (TSS>0.8) and then calculating the weighted average based on their TSS values to generate an ensembled occurrence probability map of species. On the map, higher probabilities indicate a greater likelihood of suitable habitat for the species. The probability corresponding to the maximum TSS was considered the threshold (Liu *et al.* 2013) to convert the map into a binary map of suitable and unsuitable habitats. In addition, the importance of each predictive variable for model fitting was assessed using the "getVarImp" function of the "sdm" R package. The response curve, revealing the relationship between the species occurrence probability and the variables, was generated using the "rcurve" function from the same R package.

Spatiotemporal dynamic analysis

According to the methodology outlined by Dai *et al.* (2019), changes in suitable habitats were assessed, and the generation of dynamic ranges was performed using the Combine Tool in ArcGIS as follows:

a. Vulnerable habitat: Regions of habitat currently deemed suitable but predicted to become unsuitable under the future climate scenario.

b. Increased suitable habitat: Regions of habitat currently considered unsuitable but predicted to become suitable under the future climate scenario.

c. Climate refugia: Regions of habitat currently suitable and predicted to remain suitable under the future climate scenario.

Results

Using a criterion of Pearson correlation coefficients < 0.7, the 28 predictive variables obtained earlier were narrowed down to 11 variables for constructing the prediction models. Table 1 shows the average AUC and TSS calculated from the test dataset using five algorithms, each with 100 replicates. In general, BRT, MaxEnt and SVM had good accuracy; of these, BRT showed the best performance, indicating that these models had greater prediction power. Only 112 high-performance models (TSS>0.8) were retained for the following weighted averaging to ensure highly accurate predictions. As a result, this ensemble model was employed to predict suitable habitats for *P. transarisanensis*. The habitat distribution of the entire study area is shown in Fig. 1b. It is evident that the spatial pattern is confined to areas with relatively higher altitudes, estimated to cover a total area of 1,396 km^2.

Table 1 The area under the curve for the receiver operating characteristic (AUC) and true skill statistic (TSS) generated by five algorithms
表 1 5種演算法獲取之接收者操作特徵曲線下面積 (receiver operating characteristic, ROC) 與真實技能統計值 (true skill statistic, TSS)

Algorithm	AUCmean	SD	TSSmean	SD
Boosted regression	0.89	0.07	0.74	0.11
Generalized L model	0.86	0.06	0.69	0.11
Multivariate adaptive regression splines	0.84	0.10	0.67	0.13
Maximum entropy	0.89	0.06	0.72	0.10
Support vector machine	0.88	0.07	0.71	0.12

SD: standard deviation

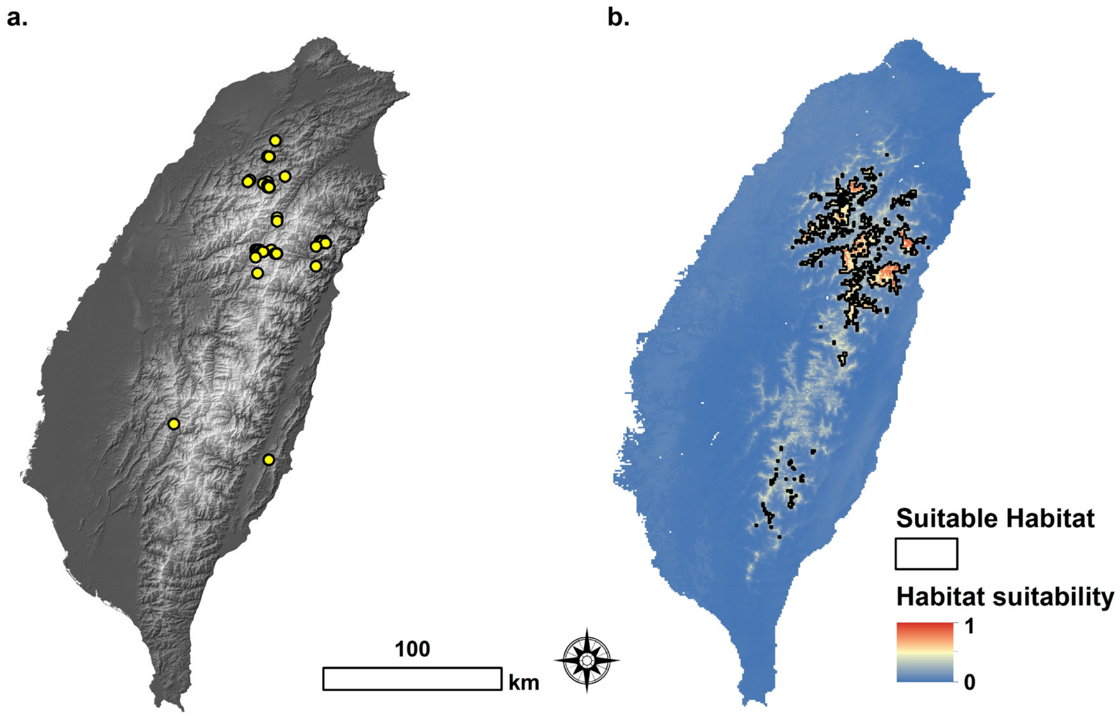

Fig. 1 (a) Occurrence records of *Prunus transarisanensis*, and a digital elevation model. Brighter colors indicate higher elevations; (b) predicted results according to the ensemble model.

圖 1 (a) 阿里山櫻花 (*Prunus transarisanensis*) 發生紀錄與研究區數值高程模型，亮度愈高代表海拔愈高；(b) 集成模型所推估之適宜生育地範圍。

Taking into consideration the importance of each variable in model fit, the variables with an importance > 10% include minimum temperature of coldest month (78.82%), precipitation of warmest quarter (22.63%), slope (10.66%) and soil texture fraction silt in percent (10.19%). The effects of the remaining variables are relatively insignificant (Table 2). The climatic variables are clearly the most dominant, with the minimum temperature of the coldest month and precipitation of the warmest quarter being the two most important variables that are related to the species' occurrence in

Table 2 Estimates of importance (%) of the predictor variables to the ensemble model
表 2 各預測變項對集成模型的重要性 (%)

Variable	Importance
Minimum temperature of coldest month	78.82
Precipitation of the warmest quarter	22.63
Slope	10.66
Soil texture fraction silt in percent	10.19
Precipitation of the coldest quarter	8.38
Cation exchange capacity	8.24
Mean diurnal range	7.51
Aspect	7.02
Temperature seasonality	5.93
Soil pH	5.82
Soil texture fraction sand in percent	4.45

ensemble prediction.

The primary contributing variables from ensemble prediction indicate that the probability of occurrence was highest at the lowest minimum temperature of the coldest month and precipitation of the warmest quarter (Fig. 2). The peak value of the former variable occurred below 1°C, while that of the latter variable occurred around 700 mm. Analysis of the response curves above indicates that *P. transarisanensis* prefers a cool

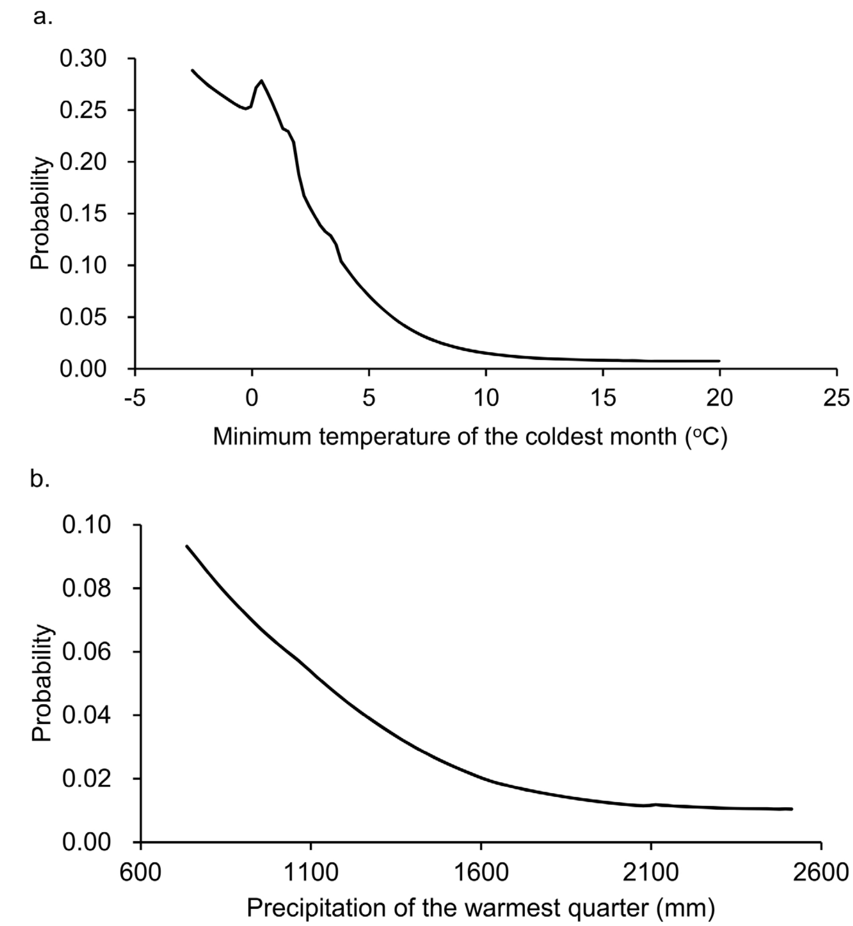

Fig. 2 Response curves of the primary contribution variables based on the ensemble prediction. (a) minimum temperature of the coldest month; (b) precipitation of the warmest quarter.
圖 2 阿里山櫻花 (*Prunus transarisanensis*) 對集成模型主要變項之反應曲線，(a) 最冷月最低溫；(b) 最暖季降水量。

environment and requires moderate precipitation.

From the current to the future, the habitat dynamic range of *P. transarisanensis* is projected. Overall, in the future, only two types of habitats will remain: climate refugia and vulnerable habitats, with the majority of the area occupied by vulnerable habitats. Under the low-emission SSP126 scenario, only a small amount of suitable habitat, estimated at approximately 355 km², can be maintained as refugia. Under the more severe warming scenarios of SSP370 and SSP585, the majority of suitable habitats are predicted to transition into vulnerable habitats, and climate refugia virtually cease to exist (Fig. 3).

Discussion

Due to its significant contribution to performance improvement, EENM is one of the most commonly used tools for predicting the impact of climate change on suitable habitats of species (Yun *et al.* 2017; Jung *et al.* 2023). The ensemble model constructed in this study was employed to predict the distribution of *P. transarisanensis*. Among the single algorithms, BRT, MaxEnt, and SVM were found to perform exceptionally well. A commonality among them is that they all belong to machine learning algorithms. Compared with the two linear models of GLM and MARS, machine learning algorithms are able to process non-linear relationships between predictors (Recknagel 2001). Therefore, this might be the reason why the models fitted by these three algorithms showed relatively better performance, as stated above. The result is similar to previous investigations on other plant species (Rahmanian *et al.* 2021; Sarma *et al.* 2022). To maintain the stability of the final model, only high-performance models are retained for the ensemble, ensuring that subsequent scenario simulations and conservation planning are built on a robust scientific foundation.

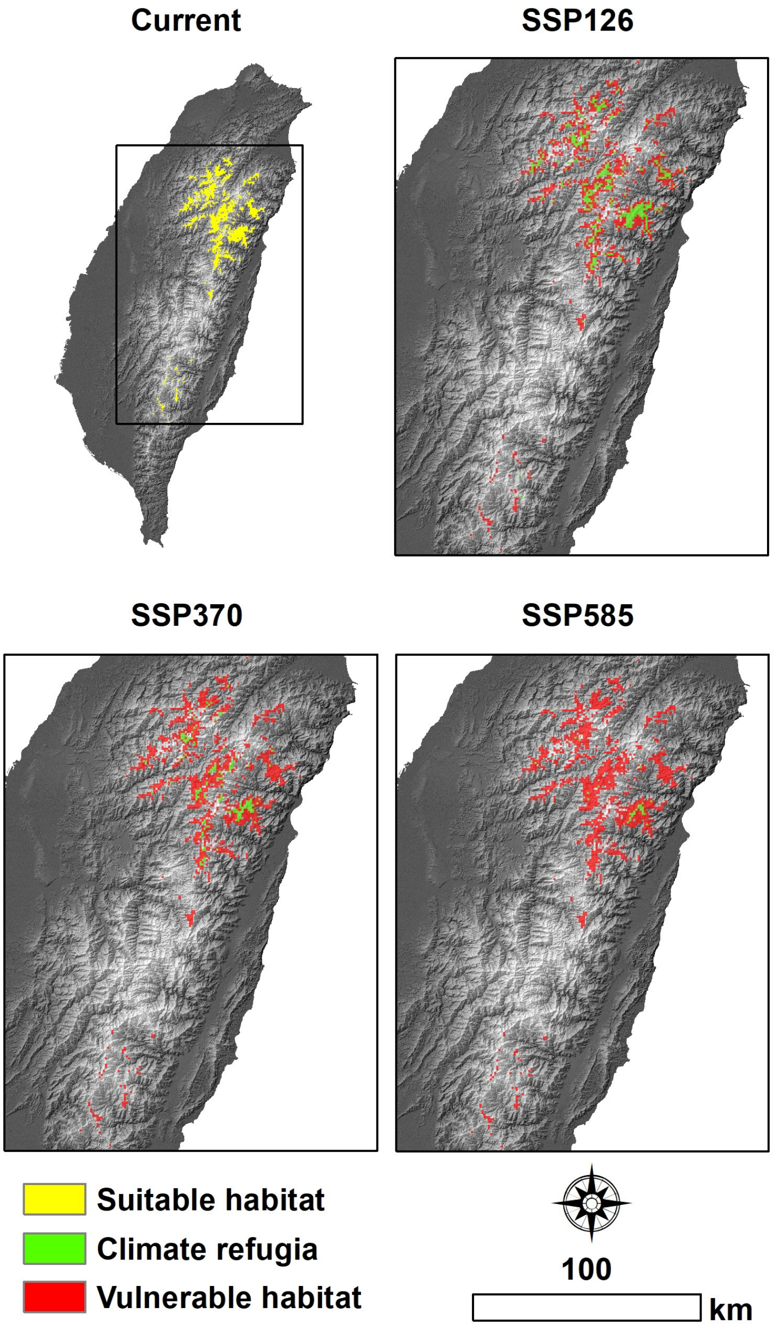

Fig. 3 The dynamic range of suitable habitat for *Prunus transarisanensis*. The upper left panel shows the current distribution, while the upper-right, bottom-left and bottom-right panels represent the SSP126, SSP370, and SSP585 emission scenarios, respectively, for the period of 2071-2100.

圖 3 阿里山櫻花 (*Prunus transarisanensis*) 的適宜生育地分布動態。左上圖為當前潛在分布，右上、左下與右下圖分別表示直至 2071~2100 年間，SSP126、SSP370 與 SSP585 情境下的潛在分布變化。

Prunus species are highly sensitive to temperature, which is one of the primary factors regulating their flowering stage. Similar to annual or biennial plants, *Prunus* species undergo a vernalization process. This involves accumulating a certain amount of chilling during endodormancy and heat during ecodormancy to ensure proper flowering in spring (Luedeling *et al.* 2013; Fadón *et al.* 2015). Therefore, maintaining a certain low-temperature level during the winter is one of the key prerequisites for their subsequent growth and development cycle (Szalay *et al.* 2010; Luedeling *et al.* 2013; Benmoussa *et al.* 2017; Zhang *et al.* 2023). The model fitting in this study indirectly supports this perspective. The ensemble model indicated that among the temperature-related variables, the minimum temperature of the coldest month strongly influenced the prediction of suitable habitat for *P. transarisanensis*. Habitats with a certain level of cold during the coldest month are relatively suitable for this species. After sufficient chill accumulation, the reproductive activity starts with inflorescence emergence as pointed out by Sakar *et al.* (2019). On the contrary, relatively high temperatures during winter may affect the tolerance limit to flowering, disrupting their phenological cycles and resulting in significant negative consequences. Additionally, a peak value is observed in the curve around 1°C, likely attributed to other variables, though it does not alter the overall trend interpretation. Besides temperature, precipitation in mountain areas is also an important factor, influencing not only plant growth but also genetic variations (Chaves *et al.* 2003; Manel *et al.* 2012). This study suggests that moderate precipitation (approximately below 1,000 mm) during the warm season is favorable for *P. transarisanensis*. Conversely, excessive precipitation may lead to adverse outcomes.

As high mountain plants have

narrow elevation tolerance, they are more exposed to a greater risk of habitat loss and local extinction due to climate change than species distributed at lower elevations (Guisan and Theurillat 2000; Engler *et al.* 2011). In this study, the species distribution predictions indicate that *P. transarisanensis* is found in the mountainous areas on the northern side of Taiwan, which have characteristics similar to temperate climate zones (Li *et al.* 2015). However, according to past climate observations, Taiwan has experienced increasing temperatures and continuous rise in extreme rainfall over the past few decades (Hsu and Chen 2002; Shiu *et al.* 2009; Jump *et al.* 2012; Tung *et al.* 2022). Therefore, the climate in Taiwan is becoming increasingly less favorable for *P. transarisanensis*, which prefers cooler and moderate precipitation environments in the mountains. This also suggests that the suitable habitat of this species is likely undergoing qualitative shifts due to climate change.

As for future projections, the results of most GCMs agree that Taiwan is highly susceptible to extreme temperatures. For instance, heatwaves are expected to intensify, becoming more frequent and prolonged. Conversely, extremely cold days are gradually disappearing (Tsai *et al.* 2023). Regarding changes in spatial patterns of temperature, the warming is more significant in high mountains than in plains, profoundly impacting ecosystems and species distributions (Lin *et al.* 2015). Additionally, precipitation distribution in various regions is significantly uneven, leading to increasing drought and flood risks (Huang *et al.* 2012). According to the analysis results of this study, the majority of suitable habitats for *P. transarisanensis* are projected to transition into vulnerable habitats due to the impact of climate change. Even under the low emission scenario (SSP126), the available area serving as climate refugia is constrained. Under the more severe emission scenarios of SSP370 and SSP585, the predicted degradation of suitable habitats is expected to be more severe, potentially leading to a high risk of extinction for this species.

In order to adapt to future climate change, this study proposes several recommendations for the conservation of *P. transarisanensis*. Firstly, in the current conservation assessment system in Taiwan at the regional level and according to the International Union for Conservation of Nature (IUCN) criteria, this species is classified as "Near Threatened," falling short of the threatened status (Editorial Committee of the Red List of Taiwan Plants 2017; IUCN 2022). However, it is important to emphasize that it is a "vulnerable species" susceptible to the impacts of climate change, which requires increased conservation efforts. Furthermore, given the potential vulnerability of habitats, immediate priority should be given to these areas for ex situ conservation. Due to the well-established conservation network in the mountainous areas of Taiwan (Tang *et al.* 2006), there is limited space available for adjusting nature reserves to maintain suitable habitats. Therefore, it is necessary to enhance long-term monitoring efforts related to climate refugia to prevent the extinction of this species. Finally, incorporating the impacts of climate change into IUCN Red List assessments could potentially alter the threat status of numerous endemic species (Trull *et al.* 2018). As a result, the research framework established in this study can be regarded as a valuable insight for evaluating other species listed in the Red List.

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