Postprint: Prediction of Potential Suitable Habitats for the Endangered Karst Obligate Plant Excentrodendron tonkinense in China

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Abstract

Excentrodendron tonkinensis is a constructive species of karst seasonal rainforests and a karst obligate tree species, designated as a national Class II key protected wild plant and an IUCN endangered plant, with extremely high ecological and economic value. However, understanding of how its potential suitable habitat will change under global change scenarios and the key driving factors remains insufficient, affecting scientific conservation and utilization of this species. To address this, this study employs the Maximum Entropy model (MaxEnt) to analyze changes in the potential geographic distribution of E. tonkinensis in China under future climate change scenarios (SSP1-2.6 and SSP5-8.5), and tests the influence of karst geological background distribution on predictions of suitable habitats for karst obligate plants. The results indicate: (1) When incorporating karst geological background data, the average AUC value of the suitable habitat prediction model is 0.997, demonstrating good predictive performance, with model predictions strictly confined to karst regions, consistent with the karst obligate characteristics of E. tonkinensis; (2) According to model fitting results, karst geological background distribution, precipitation in the warmest season (800–950 mm), and minimum temperature in the coldest month (7–11°C) are key factors limiting the distribution of E. tonkinensis; (3) With future temperature increases, the area of potential suitable habitat for E. tonkinensis will continue to expand in karst regions, generally showing a trend of migration toward higher latitudes; parts of southwestern Guangxi and southeastern Yunnan contain relatively large areas of stable habitat. These findings demonstrate that when predicting potential geographic distribution of karst obligate plants such as E. tonkinensis, the distribution range of karst geological background must be considered; if warming continues in the future, its potential suitable habitat will expand toward higher latitudes, and the degree of endangerment may not be significantly affected by climate change; parts of southwestern Guangxi and

southeastern Yunnan represent suitable areas for conservation and utilization of E. tonkinensis under future climate change scenarios.

Full Text

Prediction of Potential Suitable Areas for the Endangered Karst Obligate Plant *Excentrodendron tonkinensis* in China

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Abstract: *Excentrodendron tonkinensis* is a constructive species of karst seasonal rainforest and an obligate karst plant, classified as a nationally second-class protected wild plant and an IUCN endangered species, with high ecological and economic value. However, understanding of how its potential suitable areas will change under global change and the key driving factors remains limited, affecting scientific conservation and utilization. This study employs the Maximum Entropy model (MaxEnt) to analyze potential geographic distribution changes in China under future climate scenarios (SSP1-2.6 and SSP5-8.5) and tests the influence of karst geological background distribution on predicting suitable areas for karst obligate plants. Results show that: (1) When karst geological background data were included, the model achieved an average AUC of 0.997, demonstrating excellent predictive performance, with results strictly confined to karst regions, consistent with the species' karst-obligate characteristics; (2) Based on model fitting, karst geological background, precipitation of the warmest quarter (800–950 mm), and minimum temperature of the coldest month (7–11 °C) are key factors limiting *E. tonkinensis* distribution; (3) With future temperature increases, the potential suitable area will continue expanding in karst regions, showing an overall trend of migration toward higher latitudes, with large stable habitats existing in parts of southwestern Guangxi and southeastern Yunnan. These findings indicate that karst geological background distribution must be considered when predicting potential geographic distributions of karst obligate plants like *E. tonkinensis*. If warming continues, its potential suitable areas will expand to higher latitudes, and the degree of endangerment may not be significantly affected by climate change. Parts of southwestern Guangxi and southeastern Yunnan represent suitable areas for conservation and utilization under future climate scenarios.

Keywords: MaxEnt model, *Excentrodendron tonkinensis*, karst obligate plants, climate change

Introduction

Species distribution is influenced by multiple environmental factors, with climate being the most important abiotic factor (Brian et al., 2019). The Sixth Assessment Report (AR6) released by the Intergovernmental Panel on Climate Change (IPCC) indicates that global mean surface temperature has risen by approximately 1 °C since 1850-1900, with average warming expected to reach or exceed 1.5 °C in the next 20 years (ZHOU et al., 2021). Climate change affects plant persistence and distribution, particularly for endangered or narrowly distributed species, as global warming may render their native habitats unable to provide stable living conditions (Bennett et al., 2019), forcing species to shift their geographic ranges to adapt. Failure to adapt may drive numerous species toward extinction (Urban, 2015). Predicting potential habitat changes and extinction risks under different future climate scenarios can provide theoretical foundations for reintroduction, conservation planning, and sustainable utilization of endangered species.

Species distribution models (SDMs) combine species occurrence data with relevant environmental variables to infer fundamental ecological niches using specific algorithms (LI et al., 2013). As SDMs can rapidly predict species distribution ranges under climate change without requiring field experimental data, they have been widely applied in endangered species conservation (Tariq et al., 2021; Guisan et al., 2005). Various methods have been proposed for constructing SDMs, including generalized linear models, generalized additive models, random forest models, bioclimatic models, and maximum entropy models, which can predict both current potential distributions and future distribution patterns under climate change (Guisan et al., 2002; LI et al., 2013). Among these, the Maximum Entropy model (MaxEnt) has become a powerful tool for predicting potential suitable areas of endangered species due to its ability to achieve high accuracy with small sample sizes and without constraints from missing distribution information (YING et al., 2016).

Excentrodendron tonkinensis is one of the main constructive species of karst seasonal rainforest (LI et al., 2008) and one of Guangxi' s three major hardwoods, possessing important ecological and economic value. Limited past conservation measures and overexploitation have severely damaged wild resources. Additionally, *E. tonkinensis* is dioecious with easily obstructed pollination, long flowering and fruiting cycles, and low seed production—only 9% of fruits produce viable seeds, with 89% being aborted (GAO et al., 2006). Consequently, populations continue declining, and the species was listed as a nationally second-class protected wild plant in the latest *List of National Key Protected Wild Plants* (National Forestry and Grassland Administration, 2021). Population recovery is crucial for maintaining stability and ecological functions of karst seasonal rainforests, requiring assessment of regional environmental adaptability and scientific prediction of ecological suitable areas to identify limiting factors and appropriate restoration zones. Existing specimen data and research show that *E. tonkinensis* naturally occurs strictly in karst regions (WEI, 2018; SU et al., 1988; LIANG et al., 1988), making it a karst-obligate species. Huang et al. (2001) demonstrated that when karst endangered species are transplanted to acidic soils, significant differences appear in leaf shape, seed size, and phenology. Due to climate and geological background factors, these species cannot complete their life cycles from seed to seed in non-karst habitats.

Excentrodendron tonkinensis has weak cold resistance, with extreme low temperatures affecting seedling survival and adult tree growth rates (Department of Forestry et al., 1978). Therefore, ex-situ conservation or introduction requires understanding heat requirements and extreme low temperature thresholds, making geographic layout considerations essential. Current research focuses on ecophysiological characteristics (OU et al., 2018; OU et al., 2020; OU et al., 2017), forest management (PANG et al., 2012), and population dynamics (XIANG et al., 2013; WANG, 2012), but potential suitable distribution areas and key driving factors remain unclear. Previous SDM studies on endangered plants such as *Taxus wallichiana* var. *mairei* (LI et al., 2021), *Ostrya rehderiana* (Tang et al., 2021), *Tetraena mongolica* (DUAN et al., 2019), *Davidia involucrata* (WANG et al., 2019), and *Bretschneidera sinensis* (GONG et al., 2015) primarily considered climate factors and large-scale soil physicochemical properties. However, national soil survey data (National Soil Census Office, 1998) show that karst habitats exhibit extremely high heterogeneity, with soil physicochemical properties varying substantially at small scales. Whether commonly used large-scale soil data can effectively characterize the unique and complex habitat features of karst obligate plants like *E. tonkinensis* remains unstudied.

This study uses MaxEnt to predict current and future (2070s, 2061–2080) potential geographic distributions under SSP1-2.6 and SSP5-8.5 scenarios, testing model predictions with and without karst geological background data to reflect comprehensive karst habitat characteristics. We address: (1) What are the key driving factors limiting *E. tonkinensis* distribution? (2) How will different future climate scenarios affect potential suitable area extents? Answers will provide scientific foundations for introduction, cultivation, and sustainable management of this karst obligate plant.

1.1 Geographic Data Acquisition

Geographic data were obtained from multi-year field surveys, the Global Biodiversity Information Facility (https://www.gbif.org/), Chinese Virtual Herbarium (http://www.cvh.org.cn), National Specimen Information Infrastructure (http://www.nsii.org.cn), Plant Photo Bank of China (http://ppbc.iplant.cn), and Guangxi' s lists of specially and first-class protected ancient trees (http://www.gxzf.gov.cn). Geographic coordinates for village-level locations were supplemented using the Baidu coordinate system (http://aqsc.shmh.gov.cn/gis/getpoint.htm). Duplicate, erroneous, unclear, and cultivated occurrence records were removed. To avoid model overfitting from clustered distributions, SDM_{Toolbox2}.4 in ArcGIS 10.7 was used to create 5 km buffers, randomly retaining one valid point per buffer, yielding 81 valid distribution points (Figure 1 [Figure 1: see original paper]).

1.2 Environmental Data

Environmental data included climate, topographic, and soil factors. Climate variables (Bio1–Bio19) and topographic factors were obtained from WorldClim (https://worldclim.org/). Future climate data used WorldClim v2.1 based on CMIP6 global climate system models. To analyze distribution variation under different scenarios, low-emission (SSP1-2.6) and high-emission (SSP5-8.5) pathways were selected, representing sustainable and conventional development trajectories (O' Neill et al., 2016). The BCC-CSM2-MR model from the Beijing Climate Center, which performs well in East Asia (Wu et al., 2014), was used to simulate 2070s (2060–2080) distributions. Soil data came from the FAO World Soil Database (https://www.fao.org/); map data from the National Geomatics Center of China (http://www.ngcc.cn/); land cover data from the Institute of Geographic Sciences and Natural Resources Research (https://www.resdc.cn/); and karst geological background distribution was digitized from the 1985 "Map of Soluble Rock Types in China" (Institute of Karst Geology, 1985).

All environmental variables were masked to China in ArcGIS 10.7, converted to ASCII format at 2.5 resolution with GCS_{{{WGS}}_{{1984}}} coordinate system.

2.1 Environmental Factor Screening

To avoid multicollinearity from highly correlated variables, Pearson correlation tests were performed using SDM_{Toolbox2}.4 in ArcGIS 10.7, with jackknife tests assessing variable importance (Yang et al., 2013). Variables with correlation coefficients $|r| < 0.8$ were retained; when $|r| \geq 0.8$, the more contributive variable was kept. Preliminary analysis revealed that large-scale soil characteristic data poorly reflected karst habitat heterogeneity, so karst geological background distribution was added as a comprehensive environmental factor. After initial model fitting, variables with 0% contribution were eliminated, leaving 17 non-collinear variables for prediction (Table 1).

2.2 Model Fitting and Suitable Area Classification

Distribution and environmental data were imported into MaxEnt 3.4.4. Jackknife tests assessed variable contributions; 25% of samples were used for model validation and 75% for training; 10 replicates were run with default parameters. Prediction accuracy was evaluated using AUC values, where <0.5 indicates failure, 0.5–0.7 poor, 0.7–0.9 moderate, and 0.9–1.0 excellent performance (LI et al., 2021).

Results were imported into ArcGIS 10.7, with current climate suitability classified using natural breaks (Jenks) into four levels: unsuitable (0–0.06), low suitability (0.06–0.22), moderate suitability (0.22–0.43), and high suitability (0.43–0.81) (ZHAO et al., 2021). Future scenarios used the same classification standards based on current suitability values to obtain potential distribution patterns.

2.3 Analysis of Future Climate Scenario Suitable Areas and Stable Habitats

Using ArcGIS 10.7, overlay analysis identified stable habitat zones where high-suitability areas overlapped between current and future SSP1-2.6/SSP5-8.5 scenarios (Tang et al., 2022). Stable habitats provide consistent environmental conditions and may serve as climate refugia, holding significant conservation importance (Tang et al., 2022). To analyze land cover sources of newly suitable areas under future scenarios, expansion zones were overlaid with reclassified land cover layers to calculate proportions of each land cover type in newly suitable areas.

Results

3.1 Model Accuracy and Current Climate Suitable Areas

The model achieved an average training AUC of 0.997 ± 0.000 (Figure 2 [Figure 2: see original paper]), indicating excellent performance. Predictions showed current suitable areas strictly confined to karst regions, matching the species' karst-obligate characteristics (Figure 3 [Figure 3: see original paper]). Low-suitability areas covered 33,600 km^2, moderate-suitability areas 19,700 km^2, and high-suitability areas 14,800 km^2 (22% of total suitable area), primarily distributed in southwestern Guangxi and southeastern Yunnan karst mountains.

3.2 Environmental Factor Contributions and Adaptive Ranges

Model results identified precipitation of the warmest quarter (Bio18), karst geological background distribution (Karst), and minimum temperature of the coldest month (Bio6) as the top contributors, each exceeding 10% contribution (Table 1). Response curves indicated optimal ranges of 800–950 mm for warmest quarter precipitation and 7–11 °C for coldest month minimum temperature, with strict requirement for karst terrain (Figure 4 [Figure 4: see original paper]).

3.3 Future Climate Scenario Changes in Potential Suitable Areas

Under both 2070s scenarios, suitable areas in China shifted (Figure 5 [Figure 5: see original paper]). Compared to current conditions, high, moderate, and low suitability areas all increased under SSP1-2.6 (Table 2). Total suitable area expanded by 95.17% and 213.80% under SSP1-2.6 and SSP5-8.5, respectively (Figure 6 [Figure 6: see original paper]). Guangxi showed the largest absolute increase, followed by Yunnan (Table 3). Overall, suitable areas migrated toward higher-latitude karst regions.

Overlay analysis revealed that newly suitable areas primarily originated from forests, grasslands, and croplands (Table 4). Under both scenarios, forest land accounted for the largest proportion (>49%) of new suitable areas, followed by cropland and grassland (>19% each). Stable habitat analysis showed high-suitability overlap areas of 14,800 km^2 (SSP5-8.5) and 14,500 km^2 (SSP1-2.6) with current conditions (Figure 6 [Figure 6: see original paper]).

Discussion

4.1 Influence of Soil and Karst Geological Background on Suitable Area Simulation

Model results demonstrate that karst geological background distribution critically affects simulation accuracy for karst obligate plants. Including karst data confined potential distributions strictly to karst regions, matching the species' natural distribution. Therefore, karst geological background must be considered when using MaxEnt for karst obligate plants. Previous studies show *E. tonkinensis* naturally occurs only on limestone mountains, with soil formation strongly influenced by parent rock, creating strong links between suitable areas and karst terrain (LI et al., 2008; SU et al., 1988; Department of Forestry et al., 1978). The species has developed specialized physiological and ecological traits adapted to calcium-rich karst soils. While previous research indicated suitable soils are slightly acidic to slightly alkaline with high calcium content (Department of Forestry et al., 1978), this study found small contributions from large-scale soil pH and calcium content patterns. This likely reflects difficulty in characterizing comprehensive karst habitat features with isolated soil variables, as karst soil properties show extreme variation due to complex leaching and enrichment processes (National Soil Census Office, 1998). The FAO soil database may not capture these fine-scale variations, and northern China' s alkaline soils and loess also exhibit high pH and calcium. Additionally, climate factors typically dominate large-scale models, potentially masking local soil effects. Similar findings show that while tea plants prefer acidic soils, soil pH contributes little to global distribution models (ZHANG et al., 2019). Climate contributions generally exceed soil factors in large-scale predictions, though soil may be important at local scales.

Beyond *E. tonkinensis*, China hosts many other karst-endemic endangered species, such as *Garcinia paucinervis*, *Cephalomappa sinensis*, and *Deutzianthus tonkinensis*, found only in karst regions of Yunnan, Guizhou, Guangxi, and northern Vietnam (LIANG et al., 1988). Research indicates 1,831 karst obligate species across 654 genera and 164 families in this region (YU et al., 2017; WEI, 2018), many with important ecological and economic value. Our results demonstrate that considering karst terrain distribution is fundamental for accurate simulation and conservation planning for these species.

4.2 Main Climatic Drivers of E. tonkinensis Distribution

Climate conditions are important drivers of latitudinal and vertical distribution. Model predictions show sensitivity to warmest quarter precipitation and coldest month minimum temperature. Early observations indicated annual rainfall of 1,100–1,550 mm and January mean temperatures of 10.9–13.9 °C in Guangxi distribution areas (Department of Forestry et al., 1978), consistent with our model results. Historical introduction attempts illustrate thermal requirements and cold sensitivity: 3–4-year-old seedlings from Longzhou County transplanted to Guilin Botanical Garden died during a cold wave in January 1955 when temperatures reached -4.9 °C (daily average 2.9 °C), while 14-year-old trees in warmer Nanning produced seeds but 25-year-old trees in higher-latitude Guilin never flowered (Department of Forestry et al., 1978). These results confirm model predictions.

4.3 Impacts of Future Climate Change on E. tonkinensis Suitable Areas

Model predictions indicate future warming will significantly affect potential suitable areas. Total suitable area under SSP5-8.5 increases over 60% more than SSP1-2.6, causing large-scale migration to higher-latitude karst regions. Current natural distribution spans 22°05 –24°16 N, 105°40 –108°06 E in southwestern Guangxi, extending to southeastern Yunnan (WEI, 2018; Department of Forestry et al., 1978). Future suitable areas remain concentrated in southwestern Guangxi and southeastern Yunnan karst regions, similar to current distribution. Warming-induced suitable area expansion occurs in other endangered plant studies (YANG & LI, 2021), reflecting species' heat requirements (WAN et al., 2021; WANG et al., 2020; DU et al., 2021). As a tropical species, *E. tonkinensis* shows clear heat preference. SSP5-8.5 warming will increase heat availability at higher latitudes where extensive karst regions exist, creating migration potential. Land cover analysis shows ~50% of new suitable areas under SSP5-8.5 are forest land, suggesting warming may not increase endangerment. However, karst is fragile, and most karst regions north of current distribution lack protection and experience intense human activity and severe rocky desertification (ZHANG et al., 2011; CHEN et al., 2021). Conservation must also consider biotic interactions (diseases, pests, pollinators). Whether distribution can actually expand northward requires further research. Additionally, future climate change involves increased extreme events (Harrington et al., 2018), and model results show sensitivity to extreme low temperatures. Frequent events like the 2008 freeze (CHEN et al., 2008) could severely impact population regeneration.

4.4 Potential Land Conversion and Scientific Assessment of Future Suitable Areas

Data limitations prevented consideration of extreme climate events, which may increase in frequency and impact suitable habitats. Local microhabitat effects were not included, though karst topography changes dramatically at small scales and microhabitat niches remain undefined. The model considered only topography, soil, climate, and precipitation, excluding biotic interactions and human activities. SDMs focusing on physical factors may overestimate suitable areas by neglecting biotic interactions and dispersal, creating uncertainty. Future research should address these issues for more precise predictions.

Whether new high-latitude suitable areas are appropriate for artificial cultivation and ex-situ conservation requires further study. To reduce uncertainty, artificial propagation and ex-situ conservation should prioritize stable habitats that remain highly suitable under both current and future scenarios. Analysis of Figure 6 suggests establishing cultivation bases in southwestern Guangxi and southeastern Yunnan karst regions.

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Environmental Variables for 81 Valid Distribution Points

Environmental Variable	Description
Bio18	Precipitation of warmest quarter (mm)
Karst	Karst geological background distribution
T_{GRAVE}	Topsoil gravel content
Aspect	Aspect
T_{CACO3}	Topsoil calcium carbonate
T_{TEB}	Topsoil exchangeable base
Slope	Slope
T_{SILT}	Topsoil silt fraction
T_{{{PH}}_{{H2O}}}	Topsoil pH
Bio15	Precipitation seasonality

Note: For conservation purposes, precise coordinates of the 81 valid distribution points have been appropriately obscured, showing only three decimal places.

Note: Figure translations are in progress. See original paper for figures.