# Elevational differences of the two closely related Taxus species in sympatric, evidence from species distribution modeling

Xingtong Wu<sup>1</sup>, Minqiu Wang<sup>1</sup>, Xinyu Li<sup>1</sup>, Yadan Yan<sup>1</sup>, Minjun Dai<sup>1</sup>, Wanyu Xie<sup>1</sup>, Xiaofen Zhou<sup>1</sup>, Donglin Zhang<sup>2</sup>, and Yafeng Wen<sup>1</sup>

<sup>1</sup>Central South University of Forestry and Technology <sup>2</sup>University of Georgia

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#### Abstract

Climate change is considered to affect the species distribution deeply in time and space. Knowledge of how plant distribution responded to climate change may help us know their evolutionary history and predict ongoing environmental changes. Elevational range shifts of species in response to climate change is a common phenomenon in mountains, especially for the closely related species in sympatric. Here, we selected Taxus chinensis and Taxus mairei to explore this issue. Four types of environmental variables were used to simulate the distribution patterns, under the historical climate and future climate change scenarios, with the optimization Maxent model. We found that elevational distribution of two species has significant differences. The distribution of T. chinensis was higher than that of T. mairei. The centroid of T. chinensis and T. mairei were in Sichuan and Hunan province, respectively. Temperature and precipitation were the main factors that determine the potential distribution of the two species, and the suitable distribution area of T. chinensis was lower than T. mairei. In the future, the direction of centroid migration of two species was almost opposite, T. chinensis will shift southwest while T. mairei go northeast. Our results not only provided an insight to discriminate two sympatric species in subtropical and warm temperature zones, but also gave us an important reference for the conservation of these valuable endangered species.

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<sup>1</sup>Central South University of Forestry and Technology, Hunan, 410004, China

<sup>2</sup>University of Georgia, Athens, GA 30602-7273, USA

\*Corresponding author: Yafeng Wen

Email: wenyafeng7107@163.com

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Climate change is considered to affect the species distribution deeply in time and space. Knowledge of how plant distribution responded to climate change may help us know their evolutionary history and predict ongoing environmental changes. Elevational range shifts of species in response to climate change is a common phenomenon in mountains, especially for the closely related species in sympatric. Here, we selected *Taxus chinensis* and *Taxus mairei* to explore this issue. Four types of environmental variables were used to simulate the distribution patterns, under the historical climate and future climate change scenarios, with the optimization Maxent model. We found that elevational distribution of two species has significant differences.

The distribution of T. chinensis was higher than that of T. mairei. The centroid of T. chinensis and T. mairei were in Sichuan and Hunan province, respectively. Temperature and precipitation were the main factors that determine the potential distribution of the two species, and the suitable distribution area of T. chinensis was lower than T. mairei. In the future, the direction of centroid migration of two species was almost opposite, T. chinensis will shift southwest while T. mairei go northeast. Our results not only provided an insight to discriminate two sympatric species in subtropical and warm temperature zones, but also gave us an important reference for the conservation of these valuable endangered species.

**Keywords:** Climate change, Geographic distribution, Elevational differences, Species distribution modeling, *Taxus chinensis*,

# Taxus mairei

#### Introduction

Climate change is a major factor in the suitability of habitats for many organisms worldwide. The Quaternary period has been characterized by distinct climatic oscillations, and average global temperatures and precipitation have fluctuated dramatically between glacial and inter-glacial periods (Tsumura et al., 2020). Environmental shifts associated with climate change are altering the suitable habitat area for many organisms and species have responded to these changes via migration and/or adaptation (He et al., 2019; Liang et al., 2018; Bystriakova et al., 2014). These migrations will produce new species combinations and species interactions (Jiang et al., 2021; Wang et al., 2020; Liu et al., 2014). Meanwhile, it will threaten many species with local extinction and accelerate the reproduction of some species (Zhang et al., 2019; Faleiro et al., 2018; Hulme et al., 2017; Wiens, 2016; Elsen and Tingley, 2015; Dullinger et al., 2012; Hamann & Wang, 2006; Berry et al., 2003). Therefore, it is crucial to understand how climates could alter the distribution of the species and effectively protect the operation of the ecological systems.

Species distribution models (SDMs), which aim at predicting habitat suitability by linking species distribution data with environmental data, have been extensively used to assess the impact of climatic change on species distribution pattern and the impact of species invasion, to understand niche conservatism, to select sites for species reintroduction, and to guide a variety of conservation decisions (Thuiller et al., 2019; Elith et al., 2009: Lenoir et al., 2009). Various approaches have been developed to construct SDMs, such as Bioclim (Booth et al., 2014), Generalized Linear Models (Guisan et al., 2002), Random Forest (Breiman, 2001b), Maximum Entropy (MaxEnt) (Phillips et al., 2006), etc. Here, for the purpose of illustration, we adopt the top performers a Maximum Entropy approaches which have been widely used in the SDMs owing to its simple and clear graphical interface, the output is easy to understand, and high prediction accuracy (Elith et al., 2011; Phillips et al., 2008; Phillips et al., 2006). But the latest researches have shown that model complexity in SDMs has been recently considered as an important issue that might affect model performance (Syfert et al., 2013). Recently, Muscarella et al. (2014) developed the ENMeval R package to perform automated tuning and evaluations of species distribution models by tuning the combination of RM and FC in the Maxent algorithm. This species-specific tuning of Maxent settings can help to avoid overfitting in niche models and improve the explanatory power of the results by evaluating the validation metrics, such as delta AICc, the area under the receiver-operating characteristic curve (AUC), and omission rates, to rank models and select the "best" niche model.

Taxus are the largest and most widely distributed species in Taxaceae (Fu et al., 1999). Among these, Taxus chinensis and Taxus mairei are two endemic species in China and are mainly distributed along the warm temperate to the subtropical zone. Molecular phylogenetic analyses suggested they diverged approximately in the late Miocene (Möller et al., 2020). Previous studies have shown that the morphological characteristics of the two species were almost the same and it was difficult to distinguish them. Interestingly, it has been assumed that the elevation of T. chinensis was usually higher than T. mairei (Fu et al., 1999). However, there was a lack of research on the two species at a large scale from the perspectives of habitat and analysis of climate change impacts on their habitat to verify this phenomenon.

In this study, we gathered optimized species distribution models (SDMs) and geographical information

system software (GIS) to analyse the changing pattern of the two species distribution pattern in response to climate change, with the aims to (1) explore how the distribution of the selected two species responded to climate change and uncover the dominant environmental factors in their niche differentiation; (2) verify if the two species had elevation differences since Last inter-glacial (LIG) periods; (3) determine the conservation implications for the species. It will provide an insight to delimitate the two species in sympatric and improve our understanding of the evolutionary history of the two species.

# Methods

# Species occurrence data

Species occurrences records of *T. chinensis* and *T. mairei*were collected from the fieldwork, the Chinese Virtual Herbarium (CVH, http://www.cvh.ac.cn/), the Plant Photo Bank of China (PPBC, http://www.plantphoto.cn/), and previous studies (Liu et al., 2011; Liu et al., 2018). Then, records with obvious geographical coordinates errors were discarded, duplicate records were removed, and guaranteed only one record in the 2.5'x2.5' grid by the "spThin" package. Finally, a total of 80 records for *T. chinensis* and 164 records for *T. mairei* were retained.

# **Predictor variables**

The relevance and completeness of variables are key components in the building of SDMs (Guo et al., 2017; Zimmermann et al., 2010; Elith & Leathwick, 2009). So four types of environmental variables were selected. Nineteen bioclimatic variables from 1970 to 2000 were downloaded from WorldClim 2.0 (https://worldclim.org/data/index.html) at a 2.5 arc minutes spatial resolution. To avoid biased estimates of model coefficients and spurious significance levels resulting from multi-collinearity, we excluded highly correlated climate variables with the threshold values of 0.7 based on Pearson's correlation coefficient. According to the results of previous studies, the other three types of environmental variables (topographical, soil variables, and human influence index) also contributed to the model performance (Li et al., 2021; Guo et al., 2019). Elevation was downloaded from WorldClim 2.0, aspect and slope were extracted from Digital Elevation Model (DEM, Digital Elevation Model, http://gdex.cr.usgs.gov/gdex/), and five soil variables were downloaded from the HWSD Data (Fischer et al., 2008; Ru et al., 2006). Madella et al. (2021) and Gallardo et al. (2015) provided evidence that human pressure such as resource extraction, tourism, and infrastructure development was likely to have an effect on species distribution. Thus, we assessed the importance of the human influence index (HII, http://sedac.ciesin.columbia.edu) in this model. Finally, fifteen ecologically meaningful variables were chosen for further analysis (Table 1; Figure S1).

Furthermore, Last inter-glacial (120 000-140 000 years BP), Last Glacial Maximum (About 22 000 years ago, CCSM model), and Mid Holocene (About 6 000 years ago, CCSM model) were obtained from CMIP 5. Future bioclimatic variable data for the 2050s (2041-2060) and 2070s (2061-2080) were obtained from RCPs45 (representative concentration pathways) based on the CCSM model. However, there is no available data sets about the other three types of environmental variables in the past and future periods; therefore, as with previous studies (Lv et al., 2021; Evans et al., 2020; Zhang et al., 2019), these variables were assumed to be constant.

#### Modelling procedure

ENMeval package (Muscarella et al., 2014) was used to assess the level of model complexity by comparing the combinations between regularization multiplier (RM) and feature classes (FC). RM is set to 0.5-5.0, increasing by 0.5 each time; and a combination of 6 features, namely, L, H, LQ, LQH, LQHP, and LQHPT. The model with the lowest Akaike information criterion (AIC) value would be selected (Akaike, 1988). Then, Maxent v3.4.1 was conducted (Phillips et al., 2006) to investigate the effects of past and present climatic conditions on the *T. chinensis* and *T. mairei*. A total of 10 000 pseudo-absence records were randomly generated, and a folded cross-validation approach with 10 repetitions was adopted to evaluate predictive performances. The subsequent models were generated with a randomly selected 75% and the remaining 25% of presence data being used as training and testing data for model validation. Models were under 10 replications of bootstrap replicated run type (5,000 iterations) and other parameters with the default settings. Model performance was evaluated by the area under the receiver operating characteristics curve (AUC).

#### Changing of distribution area and Centroid transition

Based on the results from the ecological niche modeling, SDMtoolbox (Brown, 2014) in ArcGIS v10.4 were used to calculate the changes of the area between different time periods and the centroids from the historical distribution to the future distribution for the two *Taxus* species. We cross-checked the changing of the distribution area based on the previous periods to identify regions that were (i) Expansion, (ii) Unchanged, and (iii) Contraction (Hu et al., 2019). In addition, the analysis of centroid transition concentrated the species distribution into an independent central point and created a vector file depicting the magnitude and direction of changes over time (Cong et al., 2020; Hu et al., 2015).

#### Results

# Model accuracy and contributions of predictor variables

Species distribution modeling was constructed for each species to predict their geographical distributions at the present time and also at the time of the past. The optimal combination of the RM and FC of *T. chinensis* and *T. mairei* were 1/LQHPT, 0.5/LQH, respectively (delta. AICc=0) (Figure S2) according to the occurrences of each species. All models had a high predictive ability (AUC > 0.9), indicating the robustness and reliability of their predictions (Figure S3).

The relative contribution of each predictor variable suggested that the two species have different environmental requirements. Mean temperature of coldest quarter (bio11), temperature annual range (bio7), and slope were the three most important predictor variables determining the distribution of T. chinensis, while the mean temperature of coldest quarter (bio11), precipitation of warmest quarter (bio18), and elevation contributed most to the potential distribution of T. mairei. All in all, Bio11 contributed most to the two species; nevertheless, the most important factors for T. chinensis and T. mairei were different, they were bio11 and bio18, respectively (Table 1). The response curves of the occurrence probability of the two species against the mean temperature of the coldest quarter (bio11) were presented in Figure S4, which clearly showed that the two Taxusspecies have different thermal preferences, the suitable temperature is about -10-15degC for T. chinensis and -10-10degC for T. mairei with an average of 1.5degC and 4.5degC, respectively (Figure 2).

# Distribution area under different periods

The predicted potential global distribution of the two species under different climatic periods were presented in Figure 3. The suitable area of the two species shown overlap but the favorable suitable area were scarcely overlapped. *T. chinensis* were mainly distributed around the Sichuan Basin, while *T. mairei* occupied most of the region in the eastern and central of China.

There were contraction and expansion in different periods, but the favorable suitable area (0.5-1) did not shown much change from the LIG to the current periods for each species; nevertheless, it shown a decreasing trend from current to the future periods (Table 2; Figure 4). In current periods, the favorable suitable area of the *T. chinensis* and *T. mairei* were  $1.964 \times 10^5 \text{km}^2$  and  $3.074 \times 10^5 \text{km}^2$ , respectively. And the favorable suitable area of *T. chinensis* was smaller than *T. mairei* in different periods (Table 2).

# **Centroids** migration

In different periods, the centroid of *T. chinensis* was in adjacent areas between Sichuan province and Chongqing city, While *T. mairei* were in Hunan province (Figure 5). The centroid of *T. chinensis* and *T. mairei* were 107.836E/31.123N and 111.741E/28.887N in current periods(Table 3). From LIG to the current periods, the migration trend of the centroid shown that the *T. chinensis* migrated northwest and *T. mairei* migrated southwest. During LIG periods, the centroid of *T. chinensis* and *T. mairei* were 107.947E/30.786N and 112.188E/29.010N, respectively. From current to the future periods (2070s), *T. chinensis* migrated

southwest while *T. mairei* migrated northeast, the migration direction was the opposite. In the 2070s, the centroid of *T. chinensis* and *T. mairei* was 107.721E/30.763N and 111.871E/29.022N, respectively. In total, the migration distance of *T. mairei* was greater than *T. chinensis* in the same periods except for the periods from RCP2050 to RCP2070.

#### **Elevational differences**

To further elucidate the elevation differences between the two species, we calculated the average elevation during different time periods. The suitable elevation interval for the two species were 0-4 000 m based on the response curves, but the peak of the response curves was different, it was 2 500m and 500m for *T. chinensis T. mairei*, respectively (Figure S4). Furthermore, we also find the average elevation of *T. chinensis* (1 500 m) was higher than *T. mairei* (1 000 m) (Figure 2) based on the occurrence records.

From the LIG to the current periods, the elevation of T. chinensis upward about twenty-four meters while T. maireidescend approximately six meters. In the future (RCP45\_2070s), with the increase of temperature, the elevation of T. chinensis and T. mairei will continue to rise.

#### Discussion

#### Main factors affecting the distribution of the two Taxus species

T. chinensis and T. mairei are two widely distributed species in the subtropical and warm temperate zones of China, and generally, the elevation of T. chinensis is higher than T. mairei (Fu et al., 1999). Based on the biological characteristics of the two species and phenological observations, Taxus are shade-tolerant species and prefer to grow around the river (Li et al., 2021; Song, 2013). In the current study, bio11 was the most important and contributing factors for T. chinensis, so the temperature was the main factor that influencing its distribution area. While for T. mairei, bio11 was the most contribution factors, but bio18 was the most important factors. Li et al. (2021) and Liu et al. (2019) supported precipitation was the most important climatic factor that restricted the habitat distribution of the T. mairei. Poudel et al. (2012) also held that low winter and very high summer rainfall made T. mairei only distributed in the East of the Himalayas in Nepal. So precipitation was the dominant factor in shaping the distribution of the T. mairei.

It is worth mentioning that rooting conditions were the second important factor (15.586%) for T. mairei (Table 1). Ru (2006) had shown that T. mairei was suitable to live in an environment with moist, fertile soil and good water permeability. As the elevation of T. mairei is relatively low, its moisture content is ample. Therefore, good water permeability is conducive to the growth of T. mairei .

# Changes in the species distribution area

From the view of the distribution region, T. chinensis and T. mairei did not have much change from the LIG to the future (RCP45\_2070s). Though their distribution area had overlapped regions, the core habitat was rarely overlapped. T. chinensis mainly distributed around the Sichuan Basin. T. mairei mostly occupied the south of the Qinling-Daba Mountains (Li et al., 2021; Fu et al., 1999). These mountain areas not only provided a relatively stable environment for the two species but also acted as the refuge during the ice age (Zhao et al., 2019; Jiang et al., 2019; Ye et al., 2017). However, the favourable suitable area will shrink from current to the future periods for the two species, it shown that excessive temperature rise is not conducive to the growth of the two species. This result was consistent with the results of Li et al. (2021) in the study of T. mairei. In addition, for other Taxus species, Taxus cuspidata will contraction with the rising of temperature in the future (the 2050s and 2070s) (Su et al., 2018).

Previous studies have shown that species will upward and northward with the increasing of temperature, such as *Quercus lamellosa* (Guo et al., 2021), *Cyananthus* (He et al., 2019), *Quercus kerrii*(Jiang et al., 2018), wild soybean (He et al., 2016), and etc. (Gottfried et al., 2012; Felde & Grytnes, 2012). Consistently, our present study predicted upward and northward shifts for *T. mairei*, it was also consistent with the results of Li et al. (2021) and Poudel et al. (2012). Instead, *T. chinensis* shifted upward and southward. This may be due to the average elevation of south was higher than the north in China, and special topography

around the Sichuan Basin may provide a route for T. chinensis to migrate.Furthermore, Liang et al. (2018) modeled 151 representative plants in the Hengduan Mountains and its adjacent areas, it shown that the mountain plants sampled shifted upward with the increasing of the temperature, but the direction was not only northward but also shifted westward or in other directions.

# Elevational differences of the two Taxus species

T. chinensis is mainly present at altitudes above 1 500 m while T. mairei tends to occur at elevations around 1 500 m since LIG, the result was in accordance with the description of Flora of China (Fu et al., 1999). And there was not a large scale population migration between the two species from the species distribution modeling. So what may contribute to their divergence along the elevation? Closely related species are expected to show more similarity as a consequence of shared climate selection, habitat, and evolutionary history in ancient periods (Miller et al., 2019). Conversely, recent climatic selection may be species-specific, as forest trees typically have the highest adaptation in their own environment (i.e., local adaptation) and different species typically occupy different climatic niches (i.e., ecological niche differences)(Hua & Wiens, 2013; Savolainen et al., 2007). Species distribution. So long term adaption to their environment may the main factors that induced their elevational differences.

Furthermore, this phenomenon of elevational differences was also observed between the two closely related pine species, *Pinus massoniana* and *Pinus hwangshanensis* (Zhou et al., 2014; Li et al., 2010). These studies shown that species-specific and divergent climatic selection at the candidate genes played a key role in the ecological divergence of these two species and there were potential chromosomal introgression barriers. So what are the speciation mechanism of the *T. chinensis* and *T. mairei* ? Do they conform to "The ecological elevational hypothesis" (Duminil et al., 2013), "The geographic isolation hypothesis" (Couvreur et al., 2011), "allopatric speciation followed by secondary contract" or "elevational range displacement through competition"? It may be an interesting issue that warrants further research.

#### Implications for conservation and management

From current to future periods (RCP45\_2070s), the distribution area of T. chinensis and T. mairei will shrink. From the view of biological characters, they preferred a shady and humid environment (Wu & Wen, 2017). But with the rising of temperature, the climatic conditions such as strong radiation, low oxygen, drought, strong wind, and other adverse climatic conditions in high altitude areas will be more serious. These environmental factors are closely related to plant growth and fitness. Thus, these will have relatively strong physiological constraints on T. chinensis (Solomon et al., 2007). For T. mairei, rooting conditions is the second important factor in the SDMs, after precipitation. Besides, mounting researches have shown that temperature and precipitation were the main factors that affect rooting (Reich et al., 2018; Fang et al., 2017). In general, global warming will led to more precipitation on a global scale, and ultimately lead to the shits in soil moisture. So inappropriate hydrothermal conditions are not conducive to the rooting of seeds, it will be resulting in the population decline. Moreover, the anthropogenic disturbance is also stronger in the low-elevation areas than in high-elevation areas, and hence may also contribute to the contraction in species' range size. Up to all, we can establish germplasm resource nurseries to cultivate the seeds from different provenance, especially the T. chinensis that are located in high-elevation areas. Also, considering the influence of humans, in-situ should be enforced for the samples that are easily accessible. Furthermore, common garden experiments to investigate potential local adaptations should also be undertaken to facilitate future genetic studies.

#### Conclusions

Our results provide support for the description that the elevation of T. chinensis was higher than T. mairei. It may derive from long term adaption to the environment. Thus, it can act as a rule to discriminate the two species in their sympatric region. The distribution region did not have much change from LIG to the future periods, T. chinensis were mainly distributed in Sichuan Basin and surrounding mountains, and T. mairei occupied most of the mountains in eastern and central China. Our results suggested that the two species

will decrease their range as they shift upward in response to climate warming in the future periods. It is important to note that we should anticipate the potential habitat changes brought about by climate change and focus on the impact of habitat on rooting conditions in the following work of *Taxus* conservation.

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