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Differential Responses to Climate and Land-Use Changes in Threatened Chinese *Taxus* Species

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Abstract: Rapid climate and land-use changes have been considered as the foremost threat to global biodiversity. China contains more than 3500 threatened higher plants, whereas the relative influence of climate and land-use changes on these endangered plants have not been explored simultaneously under topographical constraints. Here, using *Taxus* plants as the case study genus, we simulated the distribution range of threatened species under three scenarios of current and future climate and land-use conditions under topographical constraints. We also measured the associated difference in the responses of *Taxus* species to climate and land-use changes. Our results demonstrated the substantial influence of climate and land-use changes on the distributions of *Taxus* species. However, we observed different responses of *Taxus* species to these environmental changes. The distribution range of *T. cuspidate* Siebold & Zuccarini and *T. mairei* Lemee & H. Léveillé would substantially shrink, whereas the habitat range of *T. fuana* Nan Li & R. R. Mill would sharply expand under RCP 8.5 (Representative Concentration Pathway scenarios) scenario. Meanwhile, *T. wallichiana* Zuccarini and *T. chinensis* (Pilger) Florin would experience apparent range shifts. Furthermore, topographical factors played non-negligible roles in shaping species distributions, and modifying the influence of climate and land-use changes. Together, these results provide robust evidence that even threatened species will have multiple responses to climate and land-use changes (e.g., shrinking, expanding, shifting). Our findings highlight that taking species ecological traits, habitat characteristics, and topographical constraints into account might provide valuable insights into threatened species conservation in the face of global environmental changes.

Keywords: climate and land-use changes; threatened species; *Taxus*; range; topographical constraints; shrinking; expanding; shifting; conservation

1. Introduction

In recent decades, the potential influence of rapid ongoing environmental changes on biodiversity and ecosystems have become the foremost concern for conservationists and ecologists [1–3]. It is widely believed that climate changes, such as warming, increasing drought, and extreme weather will significantly alter species distributions and habitat quality [4,5], and cause habitat degradation and biodiversity loss [6,7]. As a consequence of human activities and climate changes, global land use is quickly shifting, which can also further degrade species distributions by causing habitat loss, degradation, and fragmentation [8]. Hence, current and future climate and land-use changes have been recognized as the major threats to biodiversity and ecosystems [9–11].

However, the influence of climate and land-use changes have largely been explored independently [12,13]. In fact, climate and land-use changes are unlikely to separately affect species distributions [10,14]. Landscape structure and composition can effectively mediate the habitat availability and suitability [4,15]. Hence, climate changes affect the geographical range of a species at global and regional scales, whereas land-use changes can shape species distribution patterns at local scale [12]. In addition to climate and land use, topographical factors might further shape species distributions by redistributing hydrothermal conditions, soil attributes, and disturbance regimes [16,17]. In addition, rugged and discrete topography also provides stable refugia for threatened species under environmental changes [17,18]. Huge mountains and slopes can limit the dispersal of a species, which must move to track its climate niche [16,19,20]. Therefore, taking topographical factors into account might provide new insights into future actual range shifts of species under environmental changes [19]. A recent study demonstrated that a total of 3879 plant species have been identified as threatened plants in China [21]. However, few studies to date have focused on exploring the cumulative or synergistic influence of climatic and land-use changes on these endangered species under topographical constraints.

China harbors five *Taxus* species, which are discontinuously distributed in the mountains of eastern and southern China [22,23]. Unfortunately, *Taxus* plants have experienced severe degeneration due to human disturbance [14,23]. Hence, all *Taxus* species have been listed as endangered species and first-class national protected plants. Because of the narrow range and small viable population size, endangered plant species may be more sensitive to climate and land-use changes and thereby face extinction [24,25]. Furthermore, topographical factors may have a more powerful effect on relict plants, such as genus *Taxus* [17,19]. Therefore, identifying the effect of climate and land-use changes on endangered plants is critical for biodiversity conservation under global environmental changes.

Additionally, the responses of species to climate and land-use changes may be different across species [11,26]. For example, narrow-ranging species may be more vulnerable to land-use changes, while climate changes have a more powerful influence on broadly distributed species [27,28]. *Taxus* species have obviously distinct distribution ranges and regions. Alternatively, there are greatly systematic differences in climate, ecosystems, and evolutionary history among distribution regions of *Taxus* species. We posit that, therefore, such differences may cause the relative contribution of climate and land-use changes to vary across and within genus *Taxus* [29,30]. Despite this, to date, the relative influence of these environmental changes on different *Taxus* plants have not been investigated simultaneously.

To explore the potential responses of threatened plants to current and future environmental changes, we collect 378 species occurrence records of *Taxus* plants and relevant environmental data in China. Species distribution models are used to simulate the distributions of these species based on different scenario data of climate and land-use changes. Specially, we aim to address the following questions: (1) Can climate and land-use changes cause significant shifts in the spatial distributions of *Taxus* plants? (2) Do topographical factors modulate the influence of climate and land-use changes on *Taxus* species distributions? (3) Do the responses of *Taxus* plants to these changes vary across species?

2. Material and Methods

2.1. Selected Taxa

A total of five *Taxus* species (that is, *T. wallichiana* Zuccarini, *T. chinensis* (Pilger) Florin, *T. mairei* Lemee & H. Léveillé, *T. cuspidate* Siebold & Zuccarini, and *T. fauna* Nan Li & R. R. Mill) belonging to relict plants have been identified and recorded in China (Flora of China at (<http://foc.iplant.cn/>)). These *Taxus* plants have obviously distinct distribution regions (Figure 1). *Taxus cuspidate* only occurs sparsely in mixed conifer and conifer-deciduous broad-leaved forests of northeastern China, while *T. chinensis* and *T. mairei* are widely scattered in southern China (Flora of China, 1980). Furthermore, *T. fauna* is highly restricted to a narrow range of the Himalayas, while *T. wallichiana* occurs in Sichuan, Yunnan,

and Tibet (Flora of China at (<http://foc.iplant.cn/>)). Notably, *Taxus* plants are predominantly distributed in several specific habitat/forest types, therefore the population dispersion of these plants was largely restricted. In fact, these *Taxus* plants have been enlisted in China and the IUCN (International Union for Conservation of Nature) Red List of threatened species. Due to severe deforestation, *Taxus* plants have been listed on CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) Supplementary Materials and identified as national first-class protected plants of China.

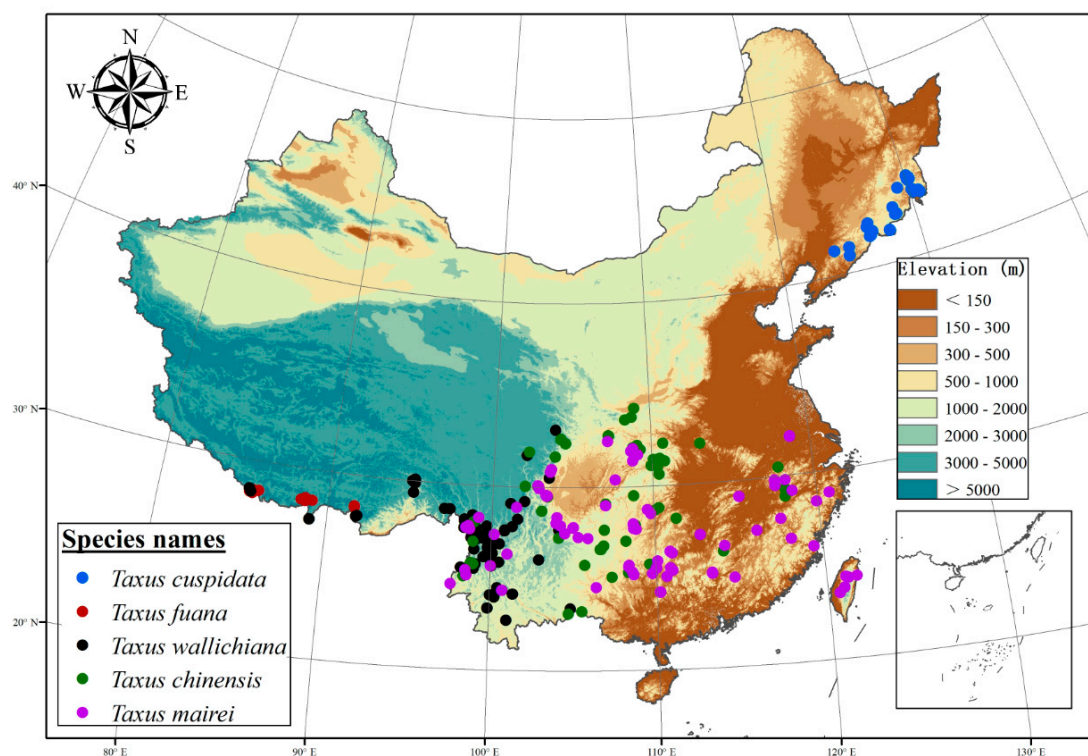


Figure 1. Locations of five *Taxus* species used in our study.

2.2. Species Occurrence Data

The occurrence data of *Taxus* plants were retrieved from (1) field observations, (2) Global Biodiversity Information Facility database (GBIF, <http://www.gbif.org>), (3) Chinese Virtual Herbarium (CVH, <http://www.cvh.ac.cn/>), (4) National Specimen Information Infrastructure (NSII, <http://www.nsii.org.cn/>), and (5) previous literature. For example, we obtained a part of the supplementary occurrence data from previous studies [22,23]. To avoid possible errors in these data, we removed the records with duplicate locations according to the relevant literature [31]. Furthermore, the records in parks, botanical gardens, and orchards were deleted [32]. After that, a total of 378 records of *Taxus* with precise coordinates were used in subsequent analysis (Figure 1 and Table 1).

Table 1. Conservation status of five *Taxus* species in the IUCN Red List and Threatened Species List of China's Higher Plant, and number of each species occurrences.

Taxon Name	IUCN 2013 Category	Category in TSLOCHP	Number of Occurrences	Latitude Ranges (°)	Elevation Ranges (m)	Geographic Ranges (km ²)
<i>T. cuspidata</i>	LC	EN	54	40.91–44.87	236–1256	48
<i>T. fuana</i>	EN	EN	12	28.36–28.67	2517–4601	10
<i>T. wallichiana</i>	EN	VU	133	22.74–33.13	533–3780	110
<i>T. chinensis</i>	EN	EN	80	23.13–34.26	158–2867	71
<i>T. mairei</i>	EN	EN	99	23.50–32.50	11–3776	87

TSLOCHP: Threatened Species List of China's Higher Plants. IUCN, International Union for Conservation of Nature.

2.3. Topography, Climate, and Land-Use Data

First, we obtained the 19 bioclimatic variables of current climate (average for 1950–2000) and future climatic conditions (using 2070) from the WorldClim global climate database (<http://www.worldclim.org>), with a resolution of 1 km × 1 km [33]. In the case of climate for 2070, our study used estimates provided by three global climate models (GCMs), including: CCSM4, MIROC5, and BCC-CSM1-1 [30,31].

The current and future land-use data with a resolution of 30 m × 30 m were derived from the Finer Resolution Observation and Monitoring–Global Land Cover (FROM-GLC Model [34]). The FROM-GLC Model provided the global land-use datasets of 2010–2100, including four Representative Concentration Pathway scenarios (RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5) with eight general land-use and land-cover types. In our study, we explored the possible conservation effects of climate and land-use changes on species distributions under three emission scenarios (RCP 2.6, RCP 4.5, and RCP 8.5). RCP 2.6 represents the most “benign” scenario, RCP 4.5 is a relatively optimistic scenario, whereas RCP 8.5 represents a pessimistic scenario. These data are freely available for download, and enable researchers to study the impacts of land-use changes at the local scale. In addition, all land-use data were resampled to the 1 km × 1 km resolution using a ‘majority’ interpolation in ArcGIS 10.2 (Version 10.2, Environmental Systems Research Institute, Redlands, United States).

Topographical variables, including elevation, slope, and aspect, were extracted/calculated from the digital elevation model (1 km × 1 km resolution) provided by Data Center for Resources and Environmental Sciences, Chinese Academy of Sciences (<http://www.resdc.cn>). The slope and aspect of the land surface were used to reflect the steepness and direction of the terrain faces [35].

2.4. Modeling Species Distributions

To avoid strong collinearity among environmental variables, the varclus procedure was conducted to evaluate the redundancy of the variables using the function “varclus” within the Hmisc package [36]. We removed any environmental variables according to the criterion: Spearman’s $\rho^2 > 0.6$, and the remaining variables were used in subsequent analysis: land use, elevation, slope, aspect, mean diurnal range (Bio2), isothermality (Bio3), minimum temperature of coldest month (Bio6), mean temperature of wettest quarter (Bio8), annual precipitation (Bio12), precipitation seasonality (Bio15), precipitation of warmest quarter (Bio18; Figure S1). The maximum entropy (MaxEnt 3.4.1) approach was applied to estimate the spatial distribution maps of individual *Taxus* plants during different periods [37]. This software can be freely downloaded from the website of the American Museum of Natural History (AMNH) (http://biodiversityinformatics.amnh.org/open_source/maxent/). It is widely observed that MaxEnt models work better with presence-only data [38,39], and both continuous and categorical variables can be input simultaneously to this model [40].

Models were conducted using two random sampling subsets of occurrence records: 80% for training data and 20% for testing data. To reduce artificial errors, we ran 500 iterations and 10 replicates using repeated split sampling for each species [41]. Furthermore, all other parameters were used according to recommended default parameters. The performance of the model for each species was examined by an area under the receiver operating characteristic curve (AUC) with the 10-fold cross-validation method [41–43]. Furthermore, AUC values were employed to evaluate the prediction accuracy of each model, and models with AUC value < 0.7 were considered as the good fitted model [44,45].

Finally, probability-occurrence results for individual species were transformed into binary categories (that is, unsuitable and suitable areas) using the threshold maximizing the sum of sensitivity and specificity (Max SSS). The Max SSS threshold can minimize the mean of the error rate and has been widely used in species distribution models [22,46]. Notably, the future geographical distributions of individual RCP were obtained by averaging the results across three global climate models. Furthermore, the relative influences of climatic, land-use, and topographical factors were calculated by using the ‘percent contribution’ (relative contributions of the covariates to model results), respectively [32,47].

2.5. Data Analyses

First, the binary species distribution models (SDMs) were converted to WGS (World Geodetic System)1984 coordinate systems within ArcMap 10.2, and then we evaluated the total area of current and future distribution maps. To explore the difference in the response of five *Taxus* species to different environmental change levels, we evaluated the stable range, gained range, and lost range for each species by contrasting current and future species distribution maps [43,48,49]. The changes in species distribution were calculated based on the difference between range gain and loss, representing species range expansion, shifting, and shrink between current and future scenarios [50]. To further assess the modifying influence of topographical factors, we ran the SDMs twice. First, we ran the SDMs using only climate and land-use variables, and then we reran the SDMs using climate, land-use, and topographical variables. We assessed the influence of topographical factors by comparing the results of two SDMs.

3. Results

3.1. Predicted Distribution of *Taxus* Plants

Mean AUC values demonstrated that all MaxEnt models (including SDMs with/without the constraints of topography, called SDMT and SDMWT after) generally exhibited an excellent predictive performance (test AUC: 0.892–0.999; training AUC: 0.943–0.999). Notably, the AUC values were overall lower in the test data than in the training data across five species model simulations.

As expected, SDMTs showed that *T. cuspidata* mainly occurred in partial regions of Jilin and Heilongjiang province (Figures 2 and 3; Figures S2–S4), while *T. fuana* was only distributed in a small area of southwest Tibet. *T. wallichiana* mainly occurred in southern Tibet, Yunnan, and Sichuan. In addition, both *T. chinensis* and *T. mairei* were widely scattered in southern China. Interestingly, the distribution range of five *Taxus* species in SDMs with the constraints of topography were greatly larger than those of SDMs with the constraints of topography (Figures 2 and 3; Figures S3–S5).

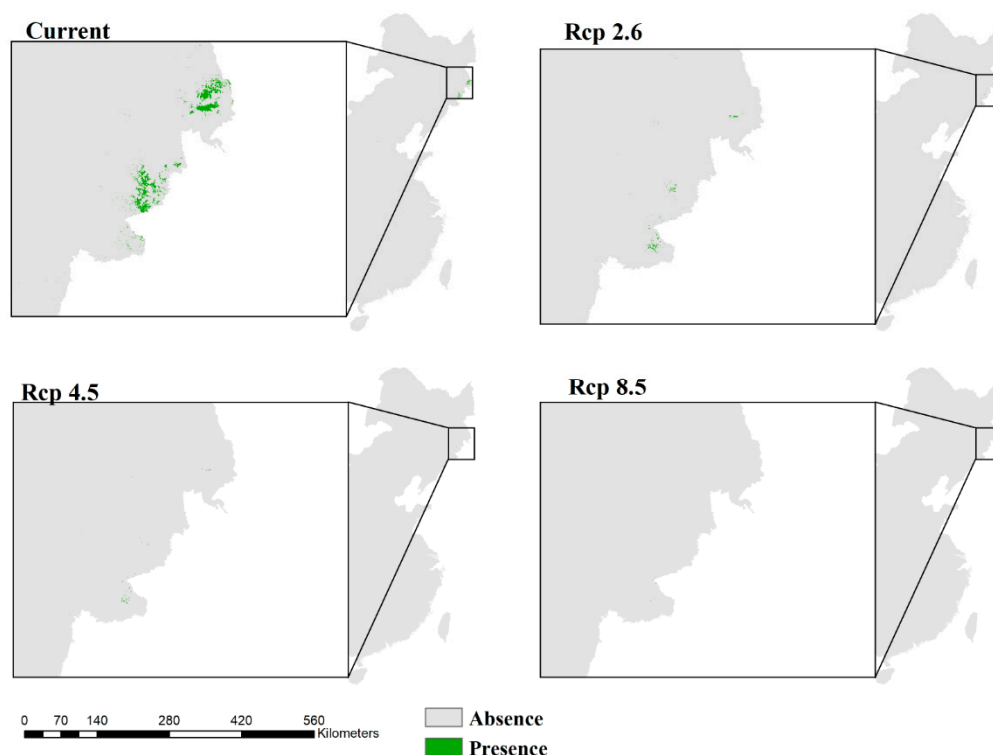


Figure 2. Binary distribution maps for *T. cuspidata* under current and future (RCP 2.6, RCP 4.5, and RCP 8.5 in 2070) environmental conditions, simulated by SDMs with the constraints of topography.

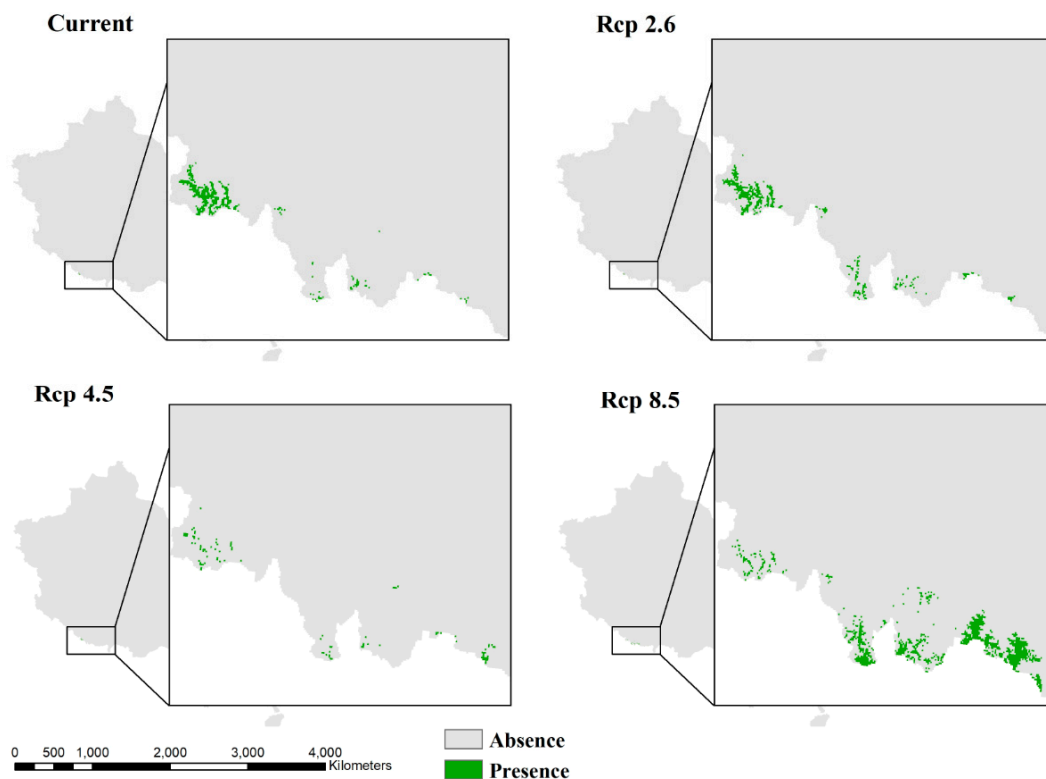


Figure 3. Binary distribution maps for *T. fuana* under current and future (RCP 2.6, RCP 4.5, and RCP 8.5 in 2070) environmental conditions, simulated by SDMs with the constraints of topography.

3.2. Changes in Species Distributions

When SDMs were constrained by topographical factors, the influence of climatic and land-use changes on *Taxus* plants varied across species (Table 2). *T. cuspidata* would almost lose all habitat range under three RCP scenarios in 2070 (>95%), which might exhibit a tendency towards extinction. While the range of *T. chinensis* and *T. mairei* declined with the average change ratio of -9.7% and -32.67% from the current environmental conditions through to 2070 under three RCP scenarios. Quite unexpectedly, *T. fuana* would experience different-level changes under three RCP scenarios, with the change ratios of -0.08% , -73.69% , and 149.56% under RCP 2.6, RCP 4.5, and RCP 8.5 scenarios in 2070, respectively. Meanwhile, *T. wallichiana* would slightly expand habitat range, with the average change ratio of 9.57% under three RCP scenarios in 2070, respectively.

Table 2. Projected range changes of each species under future environmental change scenarios (RCP 2.6, RCP 4.5, and RCP 8.5 in 2070).

Species	RCP 2.6		RCP 4.5		RCP 8.5	
	ARCT (%)	ARCWT (%)	ARCT (%)	ARCWT (%)	ARCT (%)	ARCWT (%)
<i>T. cuspidata</i>	−92.26	−47.07	−98.13	−69.04	−99.86	−91.66
<i>T. fuana</i>	−0.08	−11.15	−73.69	9.14	149.56	219.18
<i>T. wallichiana</i>	6.29	−3.04	12.66	4.97	9.76	14.45
<i>T. chinensis</i>	−8.00	−26.29	−10.00	−29.21	−11.12	−43.12
<i>T. mairei</i>	−20.38	−12.53	−29.23	−21.47	−48.41	−23.26

RCP: Representative Concentration Pathway scenarios, SDMs: Species distribution Models, ARCT: Area change, simulated by SDMs with the constraints of topography (SDMT); ARCWT: Area change, simulated by SDMs without the constraints of topography (SDMWT). Values in bold indicate species change ratio approximately/more than 50%.

In models without constraints of topography, all *Taxus* species would show different-level range changes, compared with the results of SDMs with the constraints of topography (Table 2). The range loss ratio of *T. cuspidata* and *T. chinensis* in SDMT was obviously higher than that in SDMWT. Conversely, *T. chinensis* could have more range loss in SDMT than in SDMWT. It was interesting that *T. fuana* would have a range loss of -73.69% , in contrast with the slight range expansion under the assumption in SDMWT.

To understand the internal range shifts of each species, we partitioned the total range changes into two components: range loss and gain (Figures 4 and 5; Figures S6–S8). The results of SDMT showed that the range loss of *T. cuspidata* and *T. mairei* was three times larger than the range gain under three RCP scenarios, which caused a substantial range shrink. Notably, the range gain of *T. fuana* was at least eight times larger than the range loss under RCP 4.5 scenarios, which resulted in a severe range shrink. Conversely, the range loss of *T. fuana* was at least three times larger than the range gain under RCP 8.5 scenarios, causing a sharp range expansion.

Although significant range loss and gain have been observed in *T. wallichiana* and *T. chinensis*, their average total range change was less than 10%, which may reflect apparent range shifting between current and future scenarios. Furthermore, the range of *T. fuana* only changed slightly under RCP 2.6 scenarios, whereas its range loss and gain remarkably occurred in different regions, which may also represent an important range shifting. In addition, the range loss and gain of the same species also differed significantly between the results of SDMT and SDMWT (Figure 6). The range loss of *T. cuspidata* in SDMT was significantly larger than that in SDWT, while *T. fuana* would lose or gain a larger range in SDMWT than in SDMT. Other *Taxus* plants also had different range loss/gain between the two SMDs.

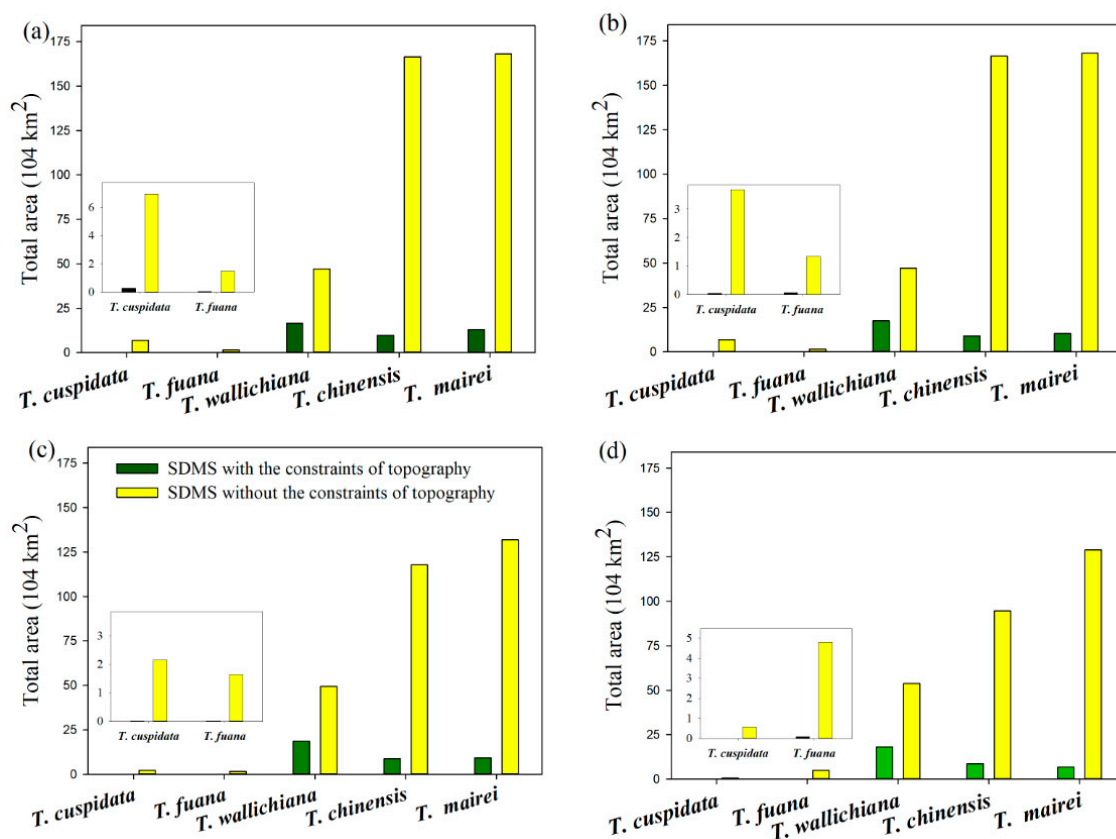


Figure 4. Total distribution area of each *Taxus* species under current (a) and future conditions (RCP 2.6 (b), RCP 4.5 (c), and RCP 8.5 (d) scenarios in 2070).

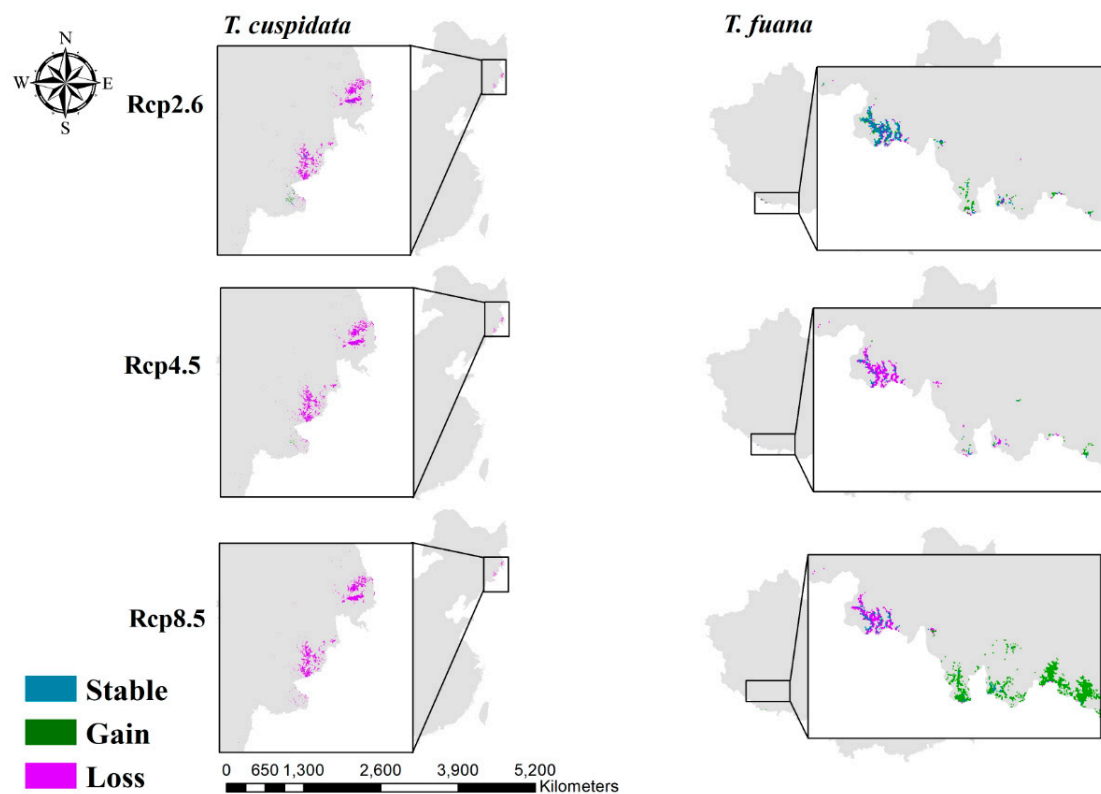


Figure 5. Spatial changes in the distribution ranges for *T. cuspidata* and *T. fuana* between current and future environmental conditions, simulated by SDMs with the constraints of topography.

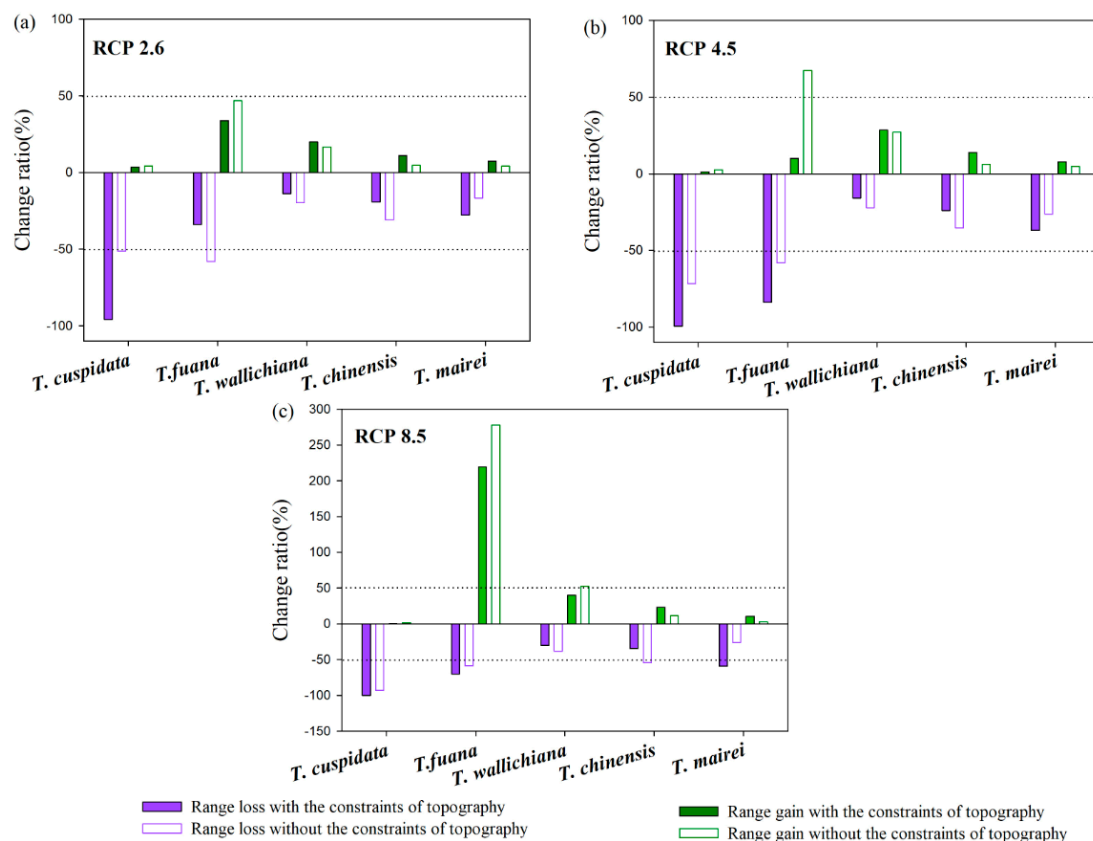


Figure 6. The range loss and gain components for each species between SDMT and SDMWT.

3.3. Relative Influence of Climate, Land-Use, and Topography on Species Distribution

Climatic factors together provided 37.8% to 68.1% of the cumulative contributions to all species distribution, which are the most crucial driving factors of the *T. cuspidata*, *T. fuana*, and *T. wallichiana* spatial distribution (Figure 7). Land use could also effectively affect the distribution of *Taxus* plants, and even provide the most influential individual contribution to *T. cuspidata* distribution (33.5%). Expectedly, topographical variables played a vital role in regulating all *Taxus* species distribution, and they contributed the largest average cumulative influence on the distribution of *T. chinensis* and *T. mairei* (58.7% and 46.4%), respectively.

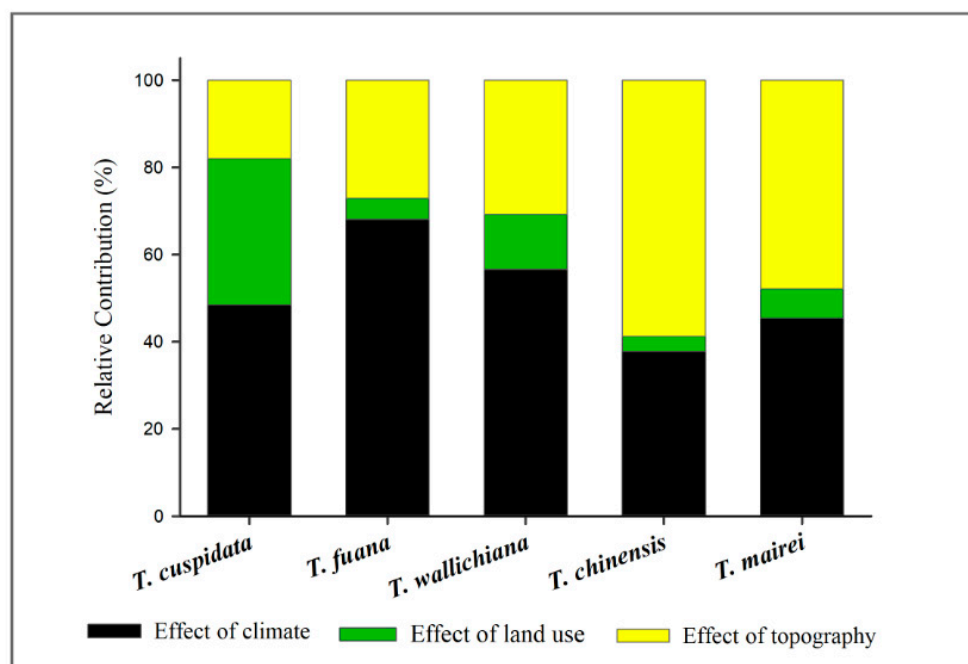


Figure 7. Relative effects of climate, land use, and topography on spatial distributions of each *Taxus* species, simulated by SDMs with the constraints of topography.

Among climatic factors, isothermality (Bio3), the minimum temperature of coldest month (Bio6) and annual precipitation (Bio12) were the most powerful climatic predictor variables, while these climatic factors had different impacts on each species (Table 3). Specifically, the minimum temperature of coldest month had the most powerful influence on *T. cuspidata* (32.7%), while the distribution of *T. fuana* and *T. wallichiana* was more strongly influenced by isothermality (59.4% and 34.5%, respectively). Finally, annual precipitation had the strongest effect on the distribution of *T. chinensis* and *T. mairei* (28.7% and 38.7%).

Table 3. Relative influence of individual variable on the distribution of each species.

Species	Contribution of the Individual Predictor (%)										
	Bio2	Bio3	Bio6	Bio8	Bio12	Bio15	Bio18	Land Use	Aspect	Altitude	Slope
<i>T. cuspidata</i>	2.1	4.2	32.7		11			33.5	11.2	5.2	1.6
<i>T. fuana</i>		59.4			4.4	1.2		4.8	27.1		
<i>T. wallichiana</i>		34.5	5.8		13.3		2.3	12.7	15	15.5	
<i>T. chinensis</i>			8.0		28.7			3.50	49.3	5.4	4.0
<i>T. mairei</i>			4.3	1.7	38.7			6.8	46.4		

Bio2, Mean Diurnal Range; Bio3, Isothermality; Bio6, Minimum Temperature of Coldest Month; Bio8, Mean Temperature of Wettest Quarter; Bio12, Annual Precipitation; Bio15, Precipitation Seasonality; Bio18, Precipitation of Warmest Quarter.

4. Discussion

4.1. The Influence of Climate and Land-Use Changes on the Spatial Distribution of *Taxus* Species

This study explored the potential influence of climate and land-use changes on five *Taxus* plants in China. This is very timely in that the threatened plants in China are facing rapid climate and land-use changes, yet still unclear to date [51,52]. Our results found significant changes in the distribution range of *Taxus* species from the current climate and land-use conditions through to future under RCP 2.6, RCP 4.5, and RCP 8.5 scenarios, and the change ratio generally increased with greenhouse gas emissions (except for *T. fuana*). This demonstrates that climate and land-use changes would cause substantial shifts in distributions of *Taxus* species, which is consistent with previous studies on common species [30].

In agreement with [30], we found that climate changes had more powerful influence (37.8%–68.1%) than land-use changes (3.5%–33.5%) on the *Taxus* species distributions, confirming the dominant role of climate changes in regulating species distributions across large spatial and temporal scales [12]. There are other interpretations for the results. First, strong covariation among climate and land-use variables makes it difficult to quantify their independent effects precisely [30]. Second, each *Taxus* species has its specific land-use preference (habitat preference). For instance, *T. cuspidate* mainly occurs in mixed conifer and conifer-deciduous broad-leaved forests, while *Taxus chinensis* is mainly distributed in evergreen and deciduous broad-leaved forests [53]. However, our land-use dataset could only be divided into relatively coarse classification levels (e.g., forest, grassland, and shrubland). Therefore, the present study may underestimate the effects of land-use changes on species distributions.

Notably, we also observed that land use could strongly shape the distribution range of *T. cuspidate* and *T. wallichiana* (33.51% and 12.7%, Table 2), while it had very weak influence on three other *Taxus* species (3.5%–6.8%). Indeed, there were systematic differences in anthropogenic disturbance and habitat attributes of the potential distribution regions for each *Taxus* species, which could partly account for different roles of land-use changes. For example, the habitats of *T. wallichiana*, especially *T. cuspidate*, have been severely destroyed by human activities, and thus land-use changes may have a more powerful influence on these two species than the three other species. Additionally, the influence of land-use changes on plant distribution has been proven to be more intense for the species at low altitudes [54,55]. Similarly, *T. cuspidate* was mainly distributed in low to middle elevation regions where land-use changes may be more important. Taken together, we suggest that the relative importance of climate and land-use changes differ remarkably across species.

It is also notable that the same *Taxus* species showed different spatial changes of distributions under different concentration scenarios. The distribution range of *T. fuana* only has a slight change under RCP 2.6, whereas its distribution areas will lose more than 70% under RCP 4.5, in contrast with the prominent range expansion under RCP 8.5 (Table 2). In addition, the ranges of the other four species shift further and more sharply under higher emission scenarios (RCP 8.5) relative to lower emission (RCP 2.6). In fact, we observed different climate and land-use changes between three concentration scenarios (Figures S9 and S10), this may largely account for the difference in the distribution range changes of each species. Therefore, these findings suggest that the selection of concentration scenarios will significantly influence the response of species to future global changes.

4.2. Important Roles of Topographical Factors in Shaping the Spatial Distribution of *Taxus*

Topography could directly and indirectly affect species distributions, especially by modifying the influence of climate and land-use changes on related species [16,46,56]. Species might not grow in the absence of suitable topographical conditions, even if climate and land-use conditions are favorable [16,56,57]. However, few studies have examined the relative influence of climate and land-use changes among different plants within the same taxonomic groups under topographical constraints [19,43]. In this study, topographical variables, including aspect and altitude, had a significant influence on species distributions across the five species, which is consistent with previous

studies [16,19]. Meanwhile, the range changes of *Taxus* species also differed significantly between SDMT and SDMWT, implying that SDMs without topographical constraints may lead to possible biased results of species distribution range. Taken together, we highlight that topographical factors may play non-negligible roles in regulating species distributions and modifying the influence of climate and land-use changes.

Interestingly, topographical factors had different impacts on the distribution of the five *Taxus* species. For instance, topography had a weaker influence on *T. cuspidate* than the other four species, and even aspect provided the largest contributions to *T. chinensis* and *T. mairei*. In fact, *T. cuspidate* mainly occurred in northeastern China, while the other four *Taxus* species largely occurred in southern or southwestern China. In southwestern China, rugged and discrete topography creates a great variety of suitable habitats, which effectively support more species' persistence under environmental changes [17,58]. Of course, such topography is also a main obstacle for species trying to track suitable new habitats [16,18]. Therefore, topographical factors have a more powerful influence on *Taxus* species distributions in southern China.

4.3. Diverse Response to Climate and Land-Use Change in Chinese *Taxus* Plants

It is widely believed that individual responses of species to environmental changes may vary across species [59]. As expected, we observed that *Taxus* species would experience three range-change ways under climatic and land-use changes, including expansion, shift, and shrink, which is consistent with previous studies [30,60]. Previous studies propose that the distribution range size of species determines their tolerance and resilience to environmental changes by affecting the quantity of resources [61–63]. Meanwhile the lack of stable refugia in distribution regions would also make species more fragile to climate and land-use changes. In this study, *T. cuspidate* covered the smallest elevation range, and there were few stable refugia in northeastern and southeastern China where *T. cuspidate* and *T. mairei* were distributed [17]. This may partly account for the high risk of extinction for the two species [64]. Conversely, *T. wallichiana* and *T. chinensis* covered a broad elevation and geographical range, and southwestern China contained the most stable refugia. Thus, these two species only experienced a habitat range shift.

Moreover, the response of species to environmental changes may also be affected by their ecological traits, such as dispersal capacity, reproductive rates, and habitat preference. For example, *T. fuana* was mainly distributed in middle altitude coniferous forests (2500–3500), covering a small geographical range, and it was warmer than other high-altitude regions of Tibet. Therefore, *T. fuana* may occupy warm-climate ecological niches, and it would still benefit from environmental changes [65]. Indeed, the distribution range of *T. fuana* would expand sharply as a result of the rapid climate warming in southwestern Tibet under RCP 8.5 scenarios, whereas it would also significantly shrink due to climate cooling under RCP 4.5 scenarios (Figure S7). Generally, these findings may suggest that even threatened species may also have multiple responses (e.g., negative and positive) to future environmental changes, and our estimates may provide useful knowledge for biodiversity conservation.

4.4. Effective Conservation for *Taxus* Even Threatened Plants in China

Previous studies believe that threatened species are more vulnerable to climate and land-use changes than other species because of their narrow geographical range, population size, and limited tolerance [55,66]. As extremely threatened plants, however, in accordance with other common species, *Taxus* species also have diverse responses (expanding, shifting, and shrinking) to future environmental changes [30]. It suggests that threatened species may be not always negatively influenced by climate and land-use changes. Furthermore, the response of species to environmental changes may be dependent on certain species ecological traits, distribution range size, and habitat characteristics [30,67]. Hence, taking species ecological traits and specific attributes of habitats into account might strengthen the effectiveness of threatened species conservation [68].

A total of 3879 plant species have been identified as threatened species in China [21]. These threatened species, with significantly different species traits and range size, are scattered in different geographic regions of China [52]. The apparent differences among species may result in various responses of these threatened plants to future climate and land-use changes [59,67,69]. Therefore, the conservation management for threatened plants should take into consideration the potential difference in responses of these plants to global environmental changes [42]. Given the expansion, shift, and shrink of *Taxus* species, we posit that current protected area networks would not effectively protect these threatened plants. Protected area networks and conservation strategies should be duly developed and adjusted according to the changes of target species.

5. Conclusions

This study represents a case study on *Taxus* species, to explore the potential influence of ongoing climate and land-use changes on the threatened plants of China. Our results demonstrate that both climate and land-use changes could significantly change the distribution range of the five *Taxus* species. However, we found diverse responses of *Taxus* species to climatic and land-use changes, including: expanding, shifting, and shrinking. We conclude that threatened species are not always negatively influenced by climatic and land-use changes, and the response of a specific species to environmental changes may be dependent on certain species' ecological traits and distribution-range attributes. Additionally, topography may play a non-negligible role in regulating the effect of environmental changes on threatened species. In conclusion, these findings may imply that future climate and land-use changes will have multiple influences (e.g., negative and positive) on threatened species. Our results also suggest the possible biased results of species distribution models without topographical constraints. Future research on the impacts of climate and land-use changes on more threatened species under topographical constraints will provide more valuable insights into threatened species conservation in China.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/10/9/766/s1>, Figure S1: Cluster analysis of the climatic variables. The analysis was performed and plotted using varclus in the Hmisc R package. Figure S2: Presence-probability distribution maps for each species under current and future (RCP 2.6, RCP 4.5, and RCP 8.5 in 2070) environmental conditions, simulated by SDMs with the constraints of topography. Figure S3: Presence-probability distribution maps for each species under current and future (RCP 2.6, RCP 4.5, and RCP 8.5 in 2070) environmental conditions, simulated by SDMs without the constraints of topography. Figure S4: Binary distribution maps for *T. wallichiana*, *T. chinensis* and *T. mairei* under current and future (RCP 2.6, RCP 4.5, and RCP 8.5 in 2070) environmental conditions, simulated by SDMs with the constraints of topography. Figure S5: Binary distribution maps for each species under current and future (RCP 2.6, RCP 4.5, and RCP 8.5 in 2070) environmental conditions, simulated by SDMs without the constraints of topography. Figure S6: Spatial changes in the distribution ranges for *T. wallichiana*, *T. chinensis* and *T. mairei* between current and future environmental conditions, simulated by SDMs with the constraints of topography. Figure S7: Spatial changes in the distribution ranges for *T. cuspidata* and *T. fuana* between current and future environmental conditions, simulated by SDMs without the constraints of topography. Figure S8: Spatial changes in the distribution ranges for *T. wallichiana*, *T. chinensis* and *T. mairei* between current and future environmental conditions, simulated by SDMs without the constraints of topography. Figure S9: Spatial change of the Bio3, Bio6, and Bio12 between 2010 and 2070 under RCP 2.6, RCP 4.5, and RCP 8.5 scenarios (predicted by BCC-CSM1-1). Figure S10: Spatial patterns of land use in 2010 and 2070 under RCP 2.6, RCP 4.5, and RCP 8.5 scenarios.

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