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Assessment of the impact of climate change on endangered conifer tree species by considering climate and soil dual suitability and interspecific competition

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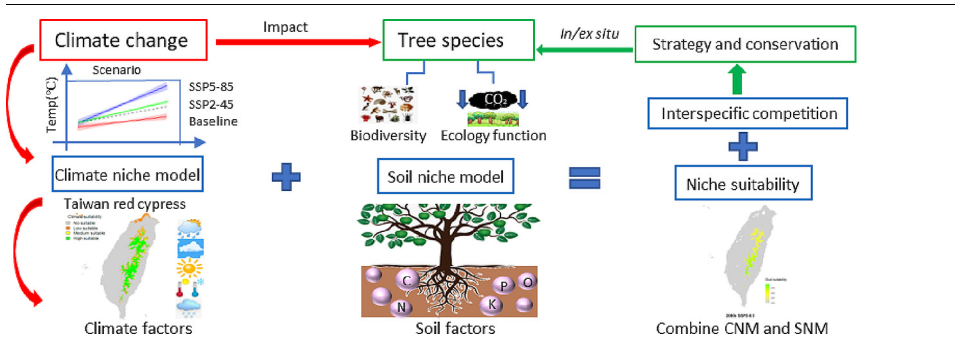
HIGHLIGHTS

- Developed a new approach that integrates soil and climate factors.
- Future dual suitable habitat for red cypress was predicted to decrease.
- Red cypress forests would face competition from late-succession oak tree species.
- Provided a framework for evaluating of the impact of climate change on endangered tree species.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate change results in the habitat loss of many conifer tree species and jeopardizes species biodiversity and forest ecological functions. Delineating suitable habitats for tree species via climate niche model (CNM) is widely used to predict the impact of climate change and develop conservation and management strategies. However, the robustness of CNM is broadly debated as it usually does not consider soil and competition factors. Here we developed a new approach to combine soil variables with CNM and evaluate interspecific competition potential in the niche overlapping areas. We used an endangered conifer species - *Chamaecyparis formosensis* (red cypress) - as a case study to predict the impact of climate change. We developed a novel approach to integrate the climate niche model and soil niche model predictions and considered interspecific competition to predict the impacts of climate change on tree species. Our results show that the suitable habitat for red cypress would decrease significantly in the future with an additional threat from the competition of an oak tree species. Our approach and results may represent significant implications in making conservation strategies and evaluating the impacts of climate change, and providing the direction of the refinement of the ecological niche model.

1. Introduction

Climate change is imposing a serious threat to global forest ecosystems and their components. An important factor behind such a threat is the mismatch between the climate that tree species (or a forest ecotype) adapted to in the past and the climate that the population will experience in the future

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(Aitken et al., 2008; Liu et al., 2022a). The mismatches are likely to lead to some tree populations stranding in sub-optimal climate conditions, which can compromise forest health, productivity, ecological functions, and even species extinction (Masson-Delmotte et al., 2021). It is predicted that climate warming by 1.5 °C could lead to around 8 % of plant species losing over half of their climatically determined geographic range (Masson-Delmotte et al., 2018), and boreal forests might be converted from carbon sinks to carbon sources (Hadden and Grelle, 2016). The impact of climate change might be particularly detrimental to some rare conifer species that adapted to low temperatures and live at high latitudes or high elevations, where climate warming is more evident (Dillon et al., 2010; Pörtner et al., 2022).

Climate niche models (CNMs), commonly called species distribution models (SDMs) or bioclimate envelope models, have been widely used to address the mismatch issues through their predictions of suitable climate habitats of forest ecosystems (Hamann and Wang, 2006; Wang et al., 2012) and forest tree species (Wang et al., 2016; Tiansawat et al., 2022) for the current and future climates. Some used CNM to guide the search for rare species or habitat conservation for endangered species (Gogol-Prokurat, 2011; Fois et al., 2018), while others used it to build forest management frameworks (Ikegami and Jenkins, 2018), predict invasive risk (Barbet-Massin et al., 2018) and plants' geographic shifts under climate change (Gogol-Prokurat, 2011; Ferrarini et al., 2019). However, the application of CNMs is under debate regarding the interpretation of the model's predictions (i.e., to be interpreted as the climate habitat vs. species distribution) (Araújo and Peterson, 2012). Also, there is a debate about the rationality of various approaches to integrate other environmental factors and species competition (Guillera-Arroita et al., 2015; Pecchi et al., 2019).

Soil is a complex ecosystem in which soil nutrition and plant roots function interactively so that each plant may have developed its own specific soil ecological niche (Sugiyama, 2019; Henneron et al., 2020). In some recent studies, both soil and climate variables were incorporated into a single niche-based model. However, this approach may compromise the weight of climatic variables or soil variables in the model contribution as the two categories of variables could be correlated (Sehler et al., 2019). Besides, the credibility of future predictions could also be compromised as soil variables need to be treated as constants for future predictions (Brun et al., 2020). For example, if climate predictors explain 80 % and soil variables explain 10 % of the total variance in a model, then only the portion of climate (80 %) can be reflected in future predictions. Therefore, developing a climate niche model and soil niche model (SNM) separately instead of merging them into a single ecological niche model has been proposed as an effective way to improve the prediction and reduce the confounding effects between soil and climate (Feng et al., 2020), in which soil niche model predictions were used as a filter to truncate climate niche model predictions. However, the way to integrate predictions from the two models may require further refining.

Interspecies competition is another factor to be considered in the use of CNMs (Pearson and Dawson, 2003; Dallas and Hastings, 2018). Although it is hard to integrate species competition into CNMs directly, it is possible to compare the CNM predictions between two species. If the climate niches of the two species overlap, they can potentially compete with each other (Adler et al., 2018; Pascual-Rico et al., 2020). Thus, the degree of ecological niche overlapping, combined with their ecological characteristics (such as regeneration ability, dominance and shade tolerance), can be used to investigate the competition possibility between two species to some extent (Pascual-Rico et al., 2020; Verhoeven et al., 2020; Pastore et al., 2021).

The *Chamaecyparis* family (commonly called Cypress) are important rare conifer species, which have been called “living fossils” because they have witnessed geological transformations, climate changes, and land changes across millions of years. Today there are only six species in the world, mainly distributed in the Asia-Pacific region, while 30 million years ago, they were ever widely distributed around the world (Council of Agriculture, 2011). However, most of the cypress family has disappeared due to the dramatic changes in climate after several glacial periods, but red cypress (*Chamaecyparis formosensis*) has survived and become a World Heritage (Council of Agriculture, 2011). Therefore, red cypress is of significance in genetic and evolutionary history research. Through our literature review from 71 references, red cypress is not only an economically important species with high physiology research values (i.e. chemical compounds extraction, growth strain study etc.) but also significant in genetic and evolutionary history research (i.e., phylogenetic, chronology and molecular genetics research, etc.) (Text S1 and Appendix S1).

Red cypress is an evergreen tree, up to 60 m tall and 6 m in diameter, and is endemic to Taiwanese mountain areas (Li, 1975). Red cypress has been listed as an endangered species by International Union for Conservation of Nature (IUCN), and its habitat has been threatened by climate change (Mu et al., 2013; Feng and Wu, 2018). However, there is a lack of large-scale research about the future distribution shift of red cypress under climate change. Although there have been sporadic studies exploring the ecological site quality model (Feng and Wu, 2018; Shao et al., 2019) or distribution models comparison (Mu et al., 2013), or physiological research on red cypress (Huang et al., 2005; Huang et al., 2021), those studies are insufficient to characterize the future suitable habitat of the red cypress. Therefore, predicting future suitable habitats for red cypress would be important from both economic and ecological perspectives under the threat of climate change.

In addition, another typical late-successional tree species, *Cyclobalanopsis longinux*, commonly called long glans oak (Wang and Chang, 1991) may become a competitor for red cypress. Long glans oak is an evergreen broad-leaved species, mainly distributed in the middle altitude (500-1800 m) (Committee, 2018), and its ecological niche with red cypress are traditionally different across the elevation gradient. However, due to climate change, the long glans oak is likely to spread to a higher elevation where red cypress is usually a dominant species. Since red cypress is a pioneer tree species, so the niche expansion of the oak trees may not be a problem in the short-term as the cedar should be able to outcompete the oak at the beginning of succession. However, the regeneration approach of red cypress is special and usually requires open and wide space (Council of Agriculture, 2011), so when considering the long-term forest succession, the expansion of long glans oak understory due to climate change may cause competition for space and resources and influence the regeneration of red cypress.

The main objective of this study is to assess the impact of climate change on the habitat of red cypress, considering both climate and soil factors and potential competition from long glans oak. Our specific research objectives were to 1) build CNM and SNM models for red cypress to predict suitable climate and soil habitat and to identify key environmental factors shaping its habitat distribution; 2) integrate CNM and SNM predictions to predict dual suitable habitat; 3) build CNM for long glans oak to predict the niche overlap between the two species and predict the competition levels in the overlapping areas. Results of this study may provide a scientific basis for the protection of endangered conifer species and the improvement of ecological niche models, as well as provide scientific support for forestry management and conservation to mitigate the impact of climate change on forest health and biodiversity.

2. Materials and methods

2.1. Species occurrence and absence data

In total, there were 1681 and 6336 occurrence records for *Chamaecyparis formosensis* (red cypress) and *Cyclobalanopsis longinux* (long glans oak), respectively (Fig. 1). The occurrence points for red cypress were generally at an altitude of about 1500–2500 m, while the records for long glans oak were mainly around 500–2000 m (Fig. 1). Those presence data were obtained from two national biological resource inventory projects: (1) National Vegetation Mapping implemented in 2003–2008 and (2) Survey of Invasive Alien Plants implemented in 2009–2012. In the first project, 3564 plots (400 m2 in size) were established and surveyed throughout Taiwan, while in the second project, another 3566 plots (125 m2) were established at low elevations and on the plains. The

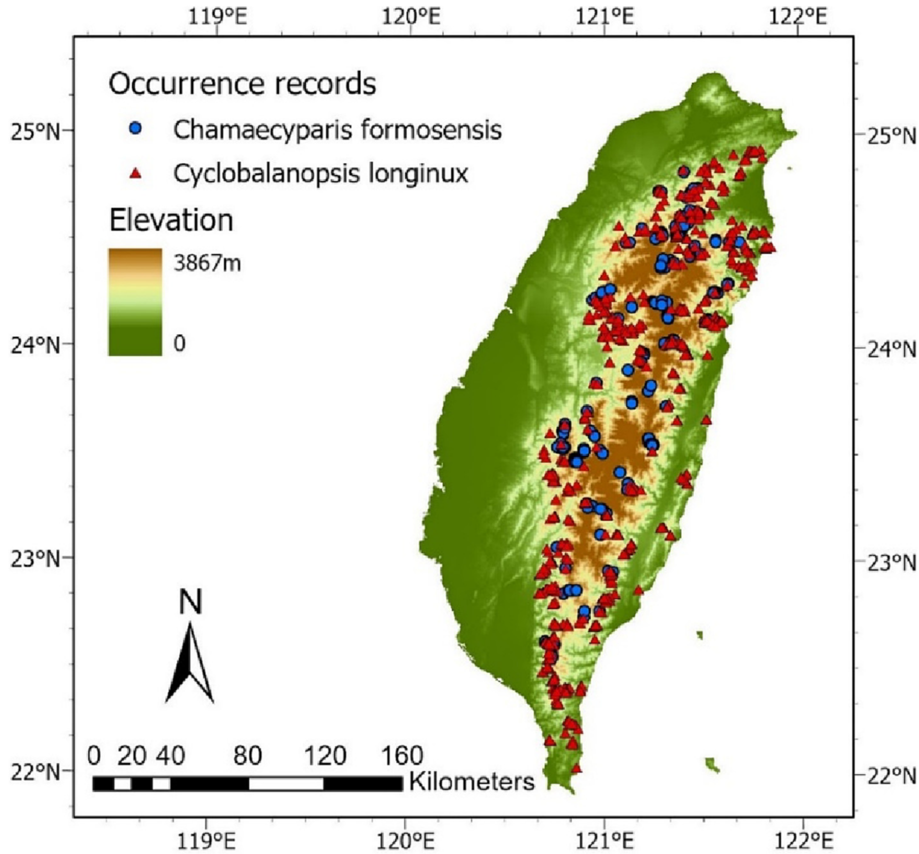

Fig. 1. Distributions of the occurrence points of *Chamaecyparis formosensis* and *Cyclobalanopsis longinux* on Taiwan island's elevation map.

inventory surveys also contained 2841 and 2370 absence points for red cypress and long glans oak, respectively.

2.2. Climate and soil data

We used ClimateAP (Wang et al., 2017) to generate climate variables for each data point of our dataset. ClimateAP uses a dynamic local downscaling algorithm to downscale gridded climate data (Daly et al., 2002; Hijmans et al., 2005) to scale-free point locations and generates a large number of climate variables for the Asia-Pacific region for historical and future periods. It has been applied to many recent studies (Zhang et al., 2018; Zhang et al., 2019; Shishir et al., 2020). We used the 1961–1990 period as a reference period and generated 54 annual and seasonal climate variables for all the presence and absence data points for model building (Appendix S2). For spatial predictions, we generated the same climate variables in raster format at 200 m × 200 m for four normal periods: 1961–1990 (reference), 2011–2040 (2020s), 2041–2070 (2050s), 2071–2100 (2080s). The future climate variables were downscaled by ClimateAP from the Coupled Model Intercomparison Project Phase 6 (CMIP6) global climate models (GCMs) with two emission scenarios of Shared Socioeconomic Pathways (SSP). We selected the 8-GCM ensembles of two climate change scenarios SSP2–4.5 and SSP5–8.5, as these two scenarios represent intermediate and high greenhouse gas (GHGs) emissions. It's predicted that SSP2–4.5 and SSP5–8.5 pathways might deliver a global mean surface air temperature increase by around 2.7 °C and 4.4 °C, respectively, in 2081–2100 (Masson-Delmotte et al., 2021).

Soil data were obtained from the World Soil Database (http://www.iiasa.ac.at/web/home/research/researchPrograms/water/HWSD.html), which includes 30 soil indicators. The 30 indicators are commonly used as soil research indicators and are divided into the top (0-30 cm) and subsoil (30-100 cm) layers, including Gravel Content, sand, silt fraction, CEC (cation exchange capacity, which describes a soil's ability to hold and exchange cations), Organic Carbon, pH value, and other physiochemical properties, etc., which are ecologically important variables (Nachtergaele et al., 2010; Wieder et al., 2014). We only used the 15 variables for the topsoil layer for this study as many areas do not have a subsoil layer in Taiwan. Those variables were derived from the raster layer at a spatial resolution of 30 arc *sec*.

2.3. Model building and statistical analysis

Modelling and statistical analysis were conducted with R software (version 3.4.3). Many modelling algorithms are used for building niche models in recent studies. Random Forest (RF) is the best performer in many studies for prediction accuracy (Cutler et al., 2007; Zhang et al., 2015; Long et al., 2021), dealing with collinearity and overfitting (Raj, 2019; Gómez-Pineda et al., 2020), handling a large number of predictors (Wang et al., 2016), and running efficiency (Behnamian et al., 2017). Thus, random forest has been considered as one of the most credible statistical methods for climatic niche model building (Rehfeldt et al., 2006; Elith and Leathwick, 2009; Wang et al., 2012). RF has high efficiency for our approach as we initially built the model with 54 climate variables and then sorted the ten key variables. We also found that using top ranking could effectively eliminate strongly correlated variables from the final model (Appendix S5-S6), so that the collinearity issue could be minimized. Therefore, we just applied RF model in this study with the default setting, in which 64 % of the original data points were used for model training, and the remaining 36 % of the data, called "out of bag" (OOB sample), were used for the evaluation of model prediction accuracy (Liaw and Wiener, 2002; Barbet-Massin et al., 2012). The percentage data for OOB sample has been testified that it can well evaluate the accuracy of model while making the most use of data (Bylander, 2002). In addition, we used the "importance" function in the RF package to rank the relative contribution of the predictor variables (Liaw and Wiener, 2002). To further improve the model accuracy, we

Table 1
OOB errors for red cypress and long glans oak niche models used in the study.

Species	Models	OOB error		
		Presence	Absence	Overall
Chamaecyparis formosensis	Climate niche model	7.8 %	4.5 %	6.3 %
	Soil niche model	7.5 %	12.4 %	9.8 %
Cyclobalanopsis longinux	Climate niche model	3.1 %	0.3 %	1.6 %

built 10 RFs, and for each RF models, we used 200 trees to grow to ensure every input row gets predicted at least a few times. The ensemble of the 10 RFs was used as the final prediction.

We applied a 2-step approach to building the climate niche models for both red cypress and long glans oak (Fig. S1). We first built an initial RF model with all 54 climate variables and identified the top 10 climate variables. We then used the ten selected climate variables and built ten forests (a "multi-forest approach") as the final model. The same approach was applied to build the soil niche model for red cypress, starting with 15 initial topsoil variables (Van Velthuizen and Verelst, 2009) and keeping the 10 top variables in the final model (Fig. S1).

To integrate soil factors in predicting the impact of climate change on red cypress distribution, there were two options: either to use the conventional approach to combine climate and soil variables and to build a combined model (Figueiredo et al., 2018) or to build a climate and soil niche models separately (Feng et al., 2020). We first tried to build a combined model using the top ten climate variables and the top ten soil variables. However, the combined model improved the model accuracy only by 0.8 % (from 93.2 % to 94.0 %) compared with the climate niche model. The importance of soil predictors was listed as the last ten important variables (Table S1), indicating that the soil effect was basically not reflected by the combined model. Thus, we chose to use the second option with modifications. Instead of simply filtering the climate niche by soil niche, we developed a new approach using "Min" function to obtain dual suitability for red cypress (Text S2). We first generated climate and soil suitability maps for red cypress from the climate and soil niche models, respectively, then we used the climate suitability as the base and overlaid the soil suitability with the "Min" function - a raster calculation algorithm, which keeps the minimum values when overlying two and more raster layers. The rationale is similar to Cannikin Law (wooden bucket effects), which is the load capacity of a bucket determined by the shortest pieces of wood rather than the longest ones. By this means, we integrated the climate suitability and soil suitability into dual suitability for the species at each grid (Fig. S2).

For the analysis of the potential competition between red cypress and long glans oak, we first calculated the presence threshold for red cypress and long glans oak based on maximum true skill statistics (TSS), which is sensitivity plus specificity minus one (Shabani et al., 2018). The presence thresholds for red cypress and long glans oak niche models were 0.48 and 0.42, respectively. We defined areas that had a probability larger than the presence threshold as "suitable" and the rest as "not suitable" for the species. Based on the suitable areas for both species, we obtained the overlapping areas between these two species, and then we used the predicted suitability of long glans oak over the overlapping areas to represent the competition potential that red cypress would face in the future. To evaluate the competition levels for red cypress in the places where red cypress already resided, we used the distribution of red cypress in the reference period and the future distribution of long glans oak to obtain the overlapping presence areas.

3. Results

3.1. Model performance and key environmental factors for red cypress

The overall OOB errors for red cypress were 6.3 % and 9.8 % for the climate niche model and the soil niche model, respectively, while for long glans oak, the overall OOB error for the climate niche model was 1.6 % (Table 1). Growing degree days for June, July, and August (DD5_jja) and reference evaporation for December, January, and February (EREF_djf) were the primary climate variables affecting red cypress distribution (Table 2). The other three of the top five variables were all related to precipitation at different seasons. The suitable range of growing degree-days for red cypress was from 422 °C to over 2, 000 °C. For the soil niche model, organic carbon (T_OC) was the most important predictor, followed by cation exchange capacity of clay (T_CEC_CLAY), Total exchangeable bases (TEB). Soil pH and base saturation were also key variables. Suitable soil organic carbon (T_OC) for red cypress ranged from 0.73 % to 3.07 % in weight, and the range of CEC_Clay was 8–52 coml kg^{-1} (Table 2).

3.2. Predicted climate suitability and dual suitability of red cypress

It was predicted that climate-suitable areas for red cypress were over 3300 km^2, accounting for 9.2 % of the total area of Taiwan islands in the reference period, and the areas were concentrated in central areas of the island (Fig. 2). The climate-suitable areas were projected to decrease with time for the periods of the 2020s, 2050s and 2080s, with only 5.2 % by

Table 2
Important climate and soil variables and their suitable ranges for the distribution of red cypress.

Type	Variables	Description	Unit	Importance	Suitable Range
Climate	DD5_jja	Summer degree-days above 5 °C, growing degree-days	°C	46.3	422– 1606
	EREF_djf	Winter Hargreaves reference evaporation	NA	32.7	38– 225
	PPT_son	Autumn precipitation	mm	30.7	315– 1122
	PPT_djf	Winter precipitation	mm	30.3	129– 528
	PPT_mam	Spring precipitation	mm	29.3	432– 1862
	TD	Continentality	°C	28.0	6.3– 11.6
	MAP	Mean annual precipitation	mm	27.5	1868– 5307
	PPT_jja	Summer precipitation	mm	25.2	722– 3225
	AHM	Annual heat:moisture index (MAT + 10)/(MAP/1000))	°C/mm	23.6	3– 14.1
	CMD_son	Autumn Hargreaves climatic moisture deficit	NA	15.5	0– 56
Soil	T_OC	Organic Carbon	% weight	14.2	0.74– 3.07
	T_CEC_CLAY	Cation Exchange Capacity(clay)	cmol/kg	11.7	8– 52
	T_TEB	Total exchangeable bases	cmol/kg	10.4	1.5– 11
	T_PH_H2O	pH of soil-water solution	-log(H +)	10.0	4.8– 6.5
	T_BS	Base Saturation	%	9.2	23– 91
	T_GRAVEL	Gravel Content	%vol.	6.7	1– 28
	T_CEC_SOIL	Cation Exchange Capacity(soil)	cmol/kg	6.4	6– 21
	T_REF_BULK_DENSITY	Reference bulk density	kg/dm3	6.0	1.25– 1.41
	T_SAND	Sand percentage	% weight	5.8	28– 51
	T_CLAY	Clay percentage	% weight	5.6	20– 50

Note: Variables end with "mam" refers to that variable for Spring (March, April, and May), while those with "jja", "son", "djf", and refers to summer (June, July, and August), autumn (September, October, November), and winter (December, January, and February) respectively.

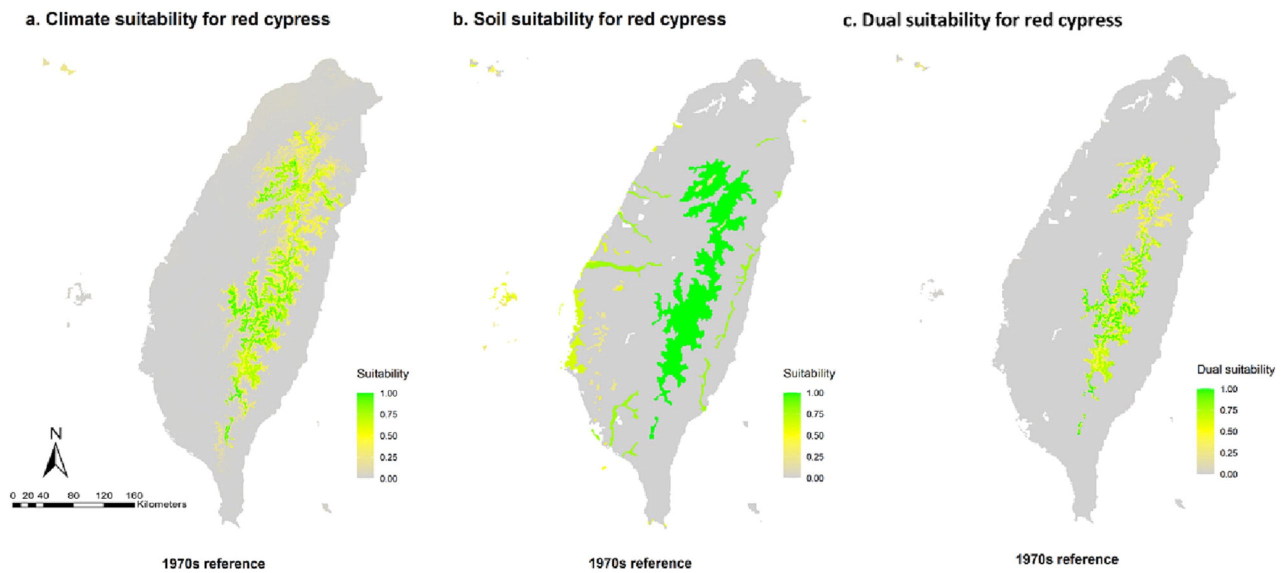

Fig. 2. Distributions of red cypress habitat of climate suitability (a), soil suitability (b), and dual suitability for both climate and soil (c) in the reference period 1961–1990. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2080s in the scenario SSP2–4.5. The decline was more pronounced in scenario SSP5–8.5, which was predicted to dip to 4.2 % by the end of this century (Table 3).

The dual suitability for red cypress also showed a declining trend with time. The suitable habitat was predicted to decrease from 6.3 % to 4.8 % for the 2080s in SSP2–4.5 (Fig. 3) and more pronounced in scenario SSP5–8.5 (to 4.0 %) for the same period (Figs. S3-S4). In comparison with only considering climate, the dual suitability-based predictions had an additional decline of 0.2–2.9 % (Table 3). It was worth noting that the suitable habitat for red cypress was predicted to become more fragmented and isolated in the future.

3.3. Predicted distribution of long glans oak and its overlaps with red cypress

Red cypress and long glans oak currently inhabit different elevations, with mean elevations of 2347.3 m and 1527.9 m, respectively (Fig. 4 and Table S2). The predicted overlapping areas between red cypress and long glans oak was 708.2 km^2, accounting for 23.5 % of suitable habitats for red cypress in the reference period (Table 4). However, the elevation of suitable climate habitat for long glans oak was projected to move up gradually to 1657.0 m on overage by the 2080s under SSP2–4.5 scenario (Table 4). The overlapping areas were predicted to increase to 44.2 % of the areas currently resided by red cypress by 2020s period and 68.7 % by 2080s under the same scenario (Fig. 5). With the SSP5–8.5 scenario, the overlapping rate was projected to increase to 78.2 % by the end of the century (Fig. S4). In general, the competition levels for the overlapping areas were predicted to increase over time, especially for the south boundary, where the suitability for the oak is expected to increase (Fig. 5).

4. Discussion

Many studies showed that rapid climate change is detrimental to some conifer species that inhabit high altitudes (Shuman et al., 2011; Bell et al., 2014; Dyderski et al., 2018). Red cypress is a species with important economic and ecological values and has attracted significant attention for genetic and evolutionary research (Supplement Text1). Therefore, evaluating the impact of climate change on suitable habitat distribution for red cypress would be valuable for forest management and conservation. As the combined model integrating soil and climate variables did not reflect soil effect, we creatively used the “Min” function to integrate the soil-suitable and climate-suitable habitats into dual suitability for red cypress. In addition, as a pioneer tree species, red cypress may eventually face competition from late-succession broadleaf species in forest succession and rehabilitation over time (Morin, 2009; West et al., 2012). Thus, we also predicted the potential challenge of the existing red cypress forests towards its potential competitor, long glans oak, and identified the vulnerable habitats in the bordering areas. Our study provided a novel approach for the assessment of climate change impact and the conservation of red cypress, which may be widely applied to the conservation and climate change adaptation for other endangered conifer species.

Table 3
Predicted areas of suitable habitats for climate and dual suitable habitats of red cypress for the reference and three periods of 2020s, 2050s, 2080s for the two climate scenarios, SSP2–4.5 and SSP5–8.5.

Scenario	Suitable areas (km2) for red cypress and percentage				
	Climate suitability	Proportion	Dual suitability	Proportion	Reduced rate (%)
1970s reference	3322.5	9.2 %	2269.4	6.3 %	2.9 %
2020s SSP2–4.5	2689.3	7.4 %	2193.7	6.1 %	1.3 %
2050s SSP2–4.5	2130.3	5.9 %	1821.5	5.0 %	0.9 %
2080s SSP2–4.5	1883.7	5.2 %	1731.4	4.8 %	0.4 %
2020s SSP5–8.5	2601.2	7.2 %	2133.4	5.9 %	1.3 %
2050s SSP5–8.5	1900.1	5.2 %	1719.8	4.8 %	0.4 %
2080s SSP5–8.5	1503.7	4.2 %	1456.4	4.0 %	0.2 %

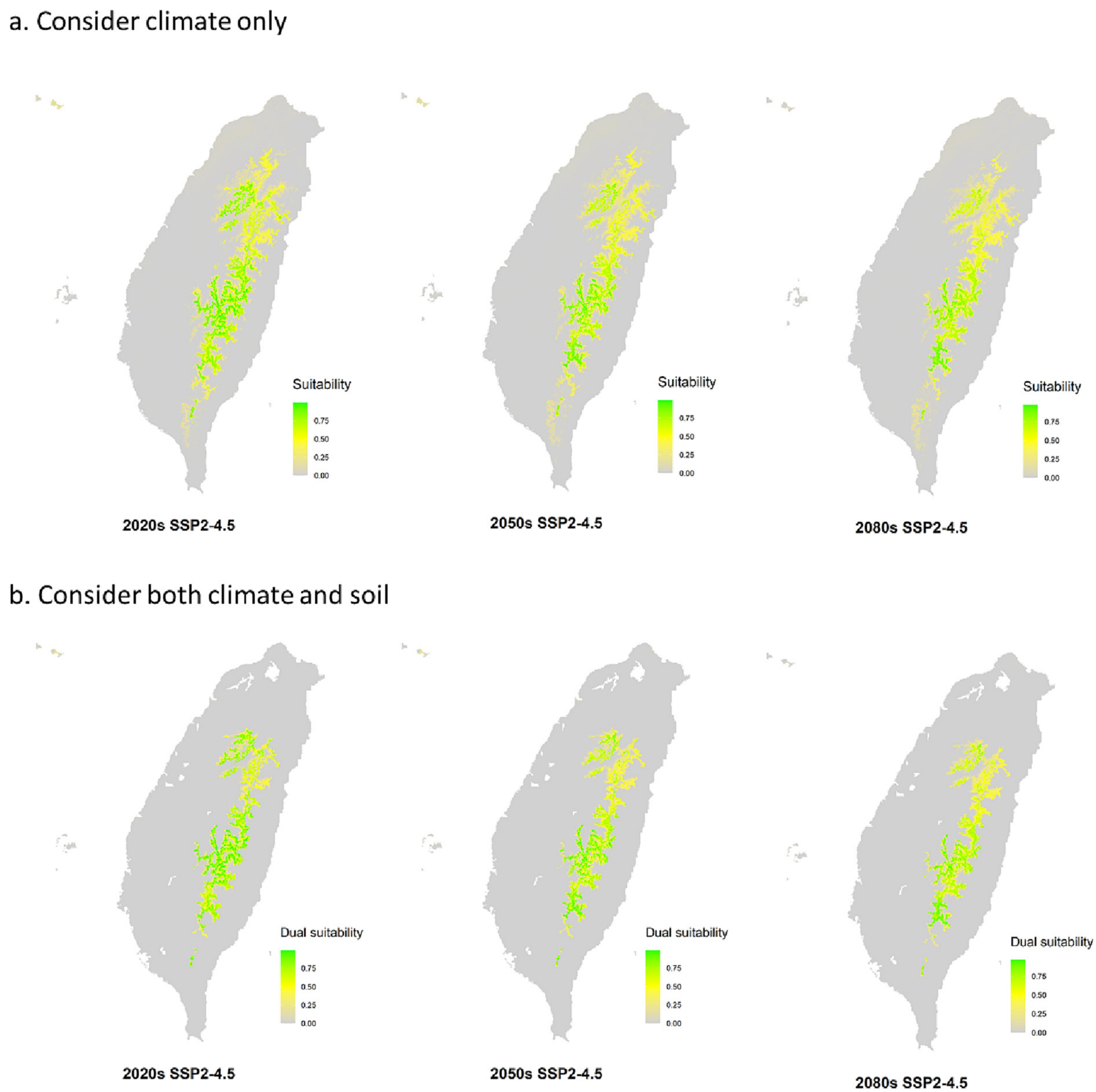

Fig. 3. Distributions of suitable habitats of red cypress for climate only (a) and dual habitat suitability for both climate and soil (b) for the three periods of 2020s, 2050s, 2080s in SSP2–4.5. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.1. Model accuracy and key climate and soil variables

Our result suggests that the climate and soil niches for red cypress can be modeled at high accuracy using Random Forest algorithm, which is consistent with other studies (Feng and Wu, 2018; Mohapatra et al., 2019; Zhang et al., 2019). Our field observation also confirms the high accuracy of our models (Appendix S3). The low error rate of our models might be attributed to the approaches that we applied based on previous studies (Barbet-Massin et al., 2012; Wang et al., 2016). These approaches include optimizing the combination of environmental variables and the use of multiple forests.

Before we built the climate and soil niche models separately, we tried to combine the top 10 climate and top 10 soil predictors into one model. We found that the accuracy of the combined model was improved by only 0.8 % compared with the climate niche model, and there were no significant correlations between the variables in the two categories (Appendix S4). This suggests that the dominant contribution of climate variables to the combined model (>90 %) is not due to their collinear relationship with the soil variables. It also shows that the combined model does not really account for the impact of soil. Therefore, building soil and climate model separately is an effective method to reflect both climate and soil suitability for tree species (Feng et al., 2020).

Identifying important environmental variables determining species distributions is useful for understanding the plant-environment relationships (Pecchi et al., 2019; Xiao et al., 2022). Our results showed that summer growing degree days (DD5_jja) and reference evaporation are primary climate variables affecting red cypress distribution, which is consistent with other studies claiming that growing degree days and evapotranspiration are key factors for the growth of conifer species (Liu and El-Kassaby, 2018). We found that seasonal precipitation was one of the ten important climate variables, suggesting that seasonal moisture changes would be crucial for the growth of red cypress. Central mountain areas in Taiwan island possess unique typography along with a typical monsoon climate that might explain why red cypress could survive while most of the cypress

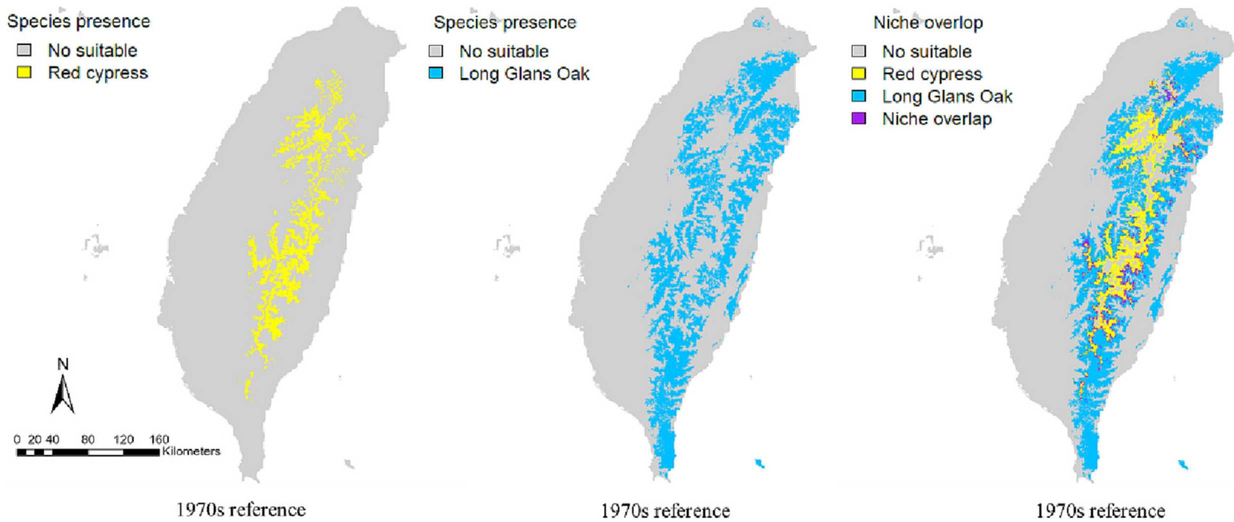

Fig. 4. Distributions of species occurrence for *Chamaecyparis formosensis* (Red cypress) (left) and *Cyclobalanopsis longinux* (Long Glans Oak) (middle) and their overlapped areas (right) in the reference period 1961–1990. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

family disappeared. In addition, the temperature difference (TD) reflecting continentality is also important for red cypress, which might be related to its phenological traits (Ettinger et al., 2020).

The ranges of SOC and CEC clay predicted by the soil niche model indicate that the areas predicted to be suitable for red cypress possessed a rich SOC with the presence of kaolinite (Table S3-S4). In addition, the soil in these areas was acidic with gravel content. Although suitable soil conditions affect the presence of tree species, the presence of tree species may also change soil conditions by changing litter composition and promoting the growth of microbial communities (Chen et al., 2020; Sokol et al., 2022). In addition, rhizosphere microorganisms can also impact the interaction between plant roots and soil nutrients (Latz et al., 2012; Liu et al., 2022b). Therefore, in developing afforestation and conservation strategies, climate factors should be regarded as the primary determining factor, while soil factors should be considered as limiting factors (Muñoz-Rojas et al., 2016; Buri et al., 2017). For endangered tree species, areas where soil and climate factors are both suitable, i.e., dual suitability areas, should be considered as potentially suitable sites for planting and conserving. In addition, further studies, i.e., investigating how tree species grow under climate and soil nutrient gradients, will also be helpful for conservation planning.

4.2. The impact of climate change on red cypress when considering soil

Similar to some pioneer conifer tree species (e.g., *Cunninghamia lanceolata, Larix decidua, Picea abies, and Pinus sylvestris*) (Dyderski et al., 2018; Xiao et al., 2022), we found that red cypress would suffer from climate change and its suitable areas would decline with time. The cause of the decline is likely related to a lack of potentially colonizable areas upward. Red cypress is a pioneer tree species and drought tolerant compared to other species (Zhu et al., 2018). So the lack of colonizable areas on the top mountain would be a serious restraint for habitat expansion under future climates, similar to what is found in other studies (Bell et al., 2014; Seastedt and Oldfather, 2021).

Table 4
Predicted areas of the suitable habitat, elevation of Long Glans Oak and their overlap percentage with red cypress for the reference and three periods of 2020s, 2050s, 2080s under two climate scenarios, SSP2–4.5 and SSP5–8.5.

Log glans oak	1970s Reference	Scenario SSP2–4.5			Scenario SSP5–8.5		
		2020s	2050s	2080s	2020s	2050s	2080s
Elevation(m)	1527.9	1608.8	1652.9	1657	1588.5	1652.7	1719.5
Area(km2)	8963.0	8782.1	8766.6	9031.7	9263.0	9057.8	8375.5
Overlap with RC[a] (km2)	780.2	1468.4	2002	2282.9	1617.7	2246.3	2598.5
Overlap percentage[b]	23.5 %	44.2 %	60.3 %	68.7 %	48.7 %	67.6 %	78.2 %

[a] RC refers to red cypress (*Chamaecyparis formosensis*).
[b] The overlap percentage was calculated by overlap area divided by the areas of existing red cypress forests in the reference period (1961–1990).

Considering only climatic factors, the suitable habitat of red cypress might be overestimated because some areas with no soil or with soil that is not suitable for red cypress. Our dual suitability approach filtered out those areas, thus, providing more credible predictions. The decline was found to be more pronounced after soil factors were considered, which is in agreement with other studies (Arruda et al., 2017; Feng et al., 2020). In addition, some plants might require specific soil conditions, e.g., soil nutrients and soil microbial communities. Therefore, predictions that consider soil factors are more comprehensive models and are supposed to be more credible in helping the conservation of rare tree species (e.g., finding new breeding sites, or high-quality provenances) (Arruda et al., 2017; Buri et al., 2017; Figueiredo et al., 2018).

It is important to notice that the current soil-related niche models treat soil factors as static for future predictions as there is no future projection available for soil variables (Brun et al., 2020; Ni and Vellend, 2022). However, soil properties are also sensitive to climate change and vegetation change. Therefore, such an assumption might compromise the credibility of future predictions to some extent, and it would be desirable to predict future species distribution reflecting the changes in soil properties in the future (Thuiller, 2013; Buri et al., 2017; Figueiredo et al., 2018).

4.3. The competition for red cypress from long glans oak

Climate change affects tree species by shifting the suitable climate niche out of the current range of tree species. Meanwhile, climate change could also affect the interaction between tree species, such as the expansion of the suitable habitat of the potential competitors nearby. Some late-succession species have been found to benefit from climate warming (Shuman et al., 2011; Dyderski et al., 2018), which might affect the understory vegetation and forest succession process at the boundary of the pioneer species. We found that the current distribution of red cypress was not much overlapped with its potential competitor long glans oak. However, climate change was projected to lead to an upward expansion of the suitable habitat of long glans oak, resulting in a dramatic increase in the overlapping areas between the two species.

The red cypress is a gymnosperm as well as pioneer species, while the long glans oak is an evergreen broadleaf species and is one of the typical

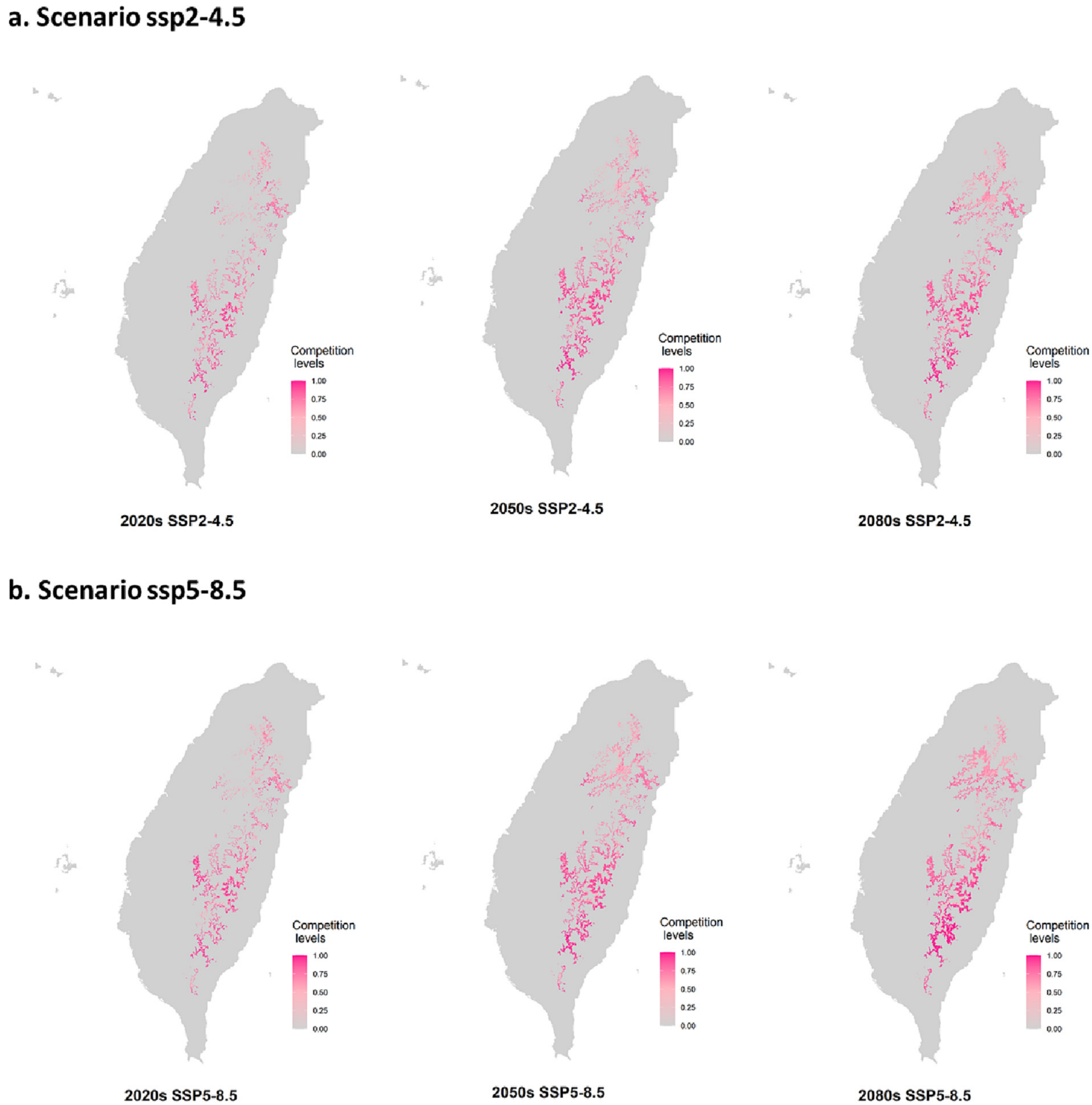

Fig. 5. Competition levels for *Chamaecyparis formosensis* (Red cypress) in the overlap areas with *Cyclobalanopsis longinux* (long glans oak) for 2020s, 2050s, 2080s in SSP2–4.5 (a) and SSP5–8.5(b) scenarios. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

late-successional species. So at the beginning of succession, the red cypress may outcompete the oak; however, for long-term forest succession long glans oak may gradually replace the red cypress and other conifer species in the process of regeneration of the mixed forest (Morin, 2009; West et al., 2012). The regeneration of red cypress usually requires a wide open space (e.g. landslide or big fallen trees Fig. S5) with sufficient sunlight (Council of Agriculture, 2011). Therefore, the expansion of the habitats of long glans oak under climate change may lead to understory vegetation changes and resource competition, eventually affecting red cypress forest regeneration. Our field observation also confirmed this point, as we observed that in the mixed forests between red cypress and long glans oak, there was not much space for small red cypress trees due to the expansion of oak trees (Fig. S6, Appendix S3).

It was found that greater species suitability was associated with a higher likelihood of presence (Dubuis et al., 2011; Noce et al., 2017). Therefore, the suitability of long glans oak can be used to represent the competition levels that red cypress would encounter. The competition levels for red cypress can be used as a reference for making conservation strategies and management policies (Booth, 2018; Srivastava et al., 2019). In addition, the competition levels can provide a reference for establishing field research stations to explore the succession, vegetation change, and the impact of climate change on natural forests. Our predictions of the niche overlapping and competition levels between species can provide important information for the assessment of climate change's impact on the forest ecosystem and species conservation (Pascual-Rico et al., 2020; Pastore et al., 2021).

5. Conclusion

The impact of climate change on forest ecology, tree health, and biodiversity will be a major challenge in this century. Such impact can be particularly serious for endangered conifer species. We used red cypress as a case study to predict the impact of climate change on suitable habitats considering climate, soil, and inter-species competition factors. We found that the impact of climate change could be underestimated if soil conditions are not considered. In addition, we found interspecies competition could impose an additional threat. Our study provides a novel approach to refine ecological niche models and evaluate interspecific competition under climate change, which could be applied to the conservation of endangered conifer tree species to mitigate the impact of climate change on forest ecology, productivity, and health.

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CRediT authorship contribution statement

Tongli Wang: Conceptualization, Methodology, Software. Wenhuan Xu.: Data curation, Writing- Original draft preparation, Visualization. Jing Jiang: Writing- Reviewing and Editing, Investigation. Huan-yu Lin: Writing- Reviewing and Editing, Data curation, Validation. Tze-Ying Chen: Data curation, Writing- Reviewing and Editing. Shiyi Zhang: Project administration.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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