

Article

Ecological Niche Overlap and Prediction of the Potential Distribution of Two Sympatric *Ficus* (Moraceae) Species in the Indo-Burma Region

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Abstract: Climate change is a major factor influencing the species distribution and population diversity of living creatures. In this study, the ecological niche model (ENM) MaxEnt was used to evaluate habitat suitability and predict potential habitats of two sympatric fig species, i.e., *Ficus squamosa* and *F. heterostyla*, in the Xishuangbanna region of China. Results indicated that mean diurnal range, isothermality, cation exchange capacity (at pH 7), and temperature seasonality were key variables influencing habitat suitability for *F. squamosa*. However, temperature seasonality and precipitation of the driest quarter showed the greatest contributions to *F. heterostyla* distribution. During the current period, the habitat suitability distributions of both *Ficus* species were considerably higher than known occurrences. In the future, potentially suitable distribution areas for both species will reduce overall across the whole study area, although some expansion may occur by 2070. Niche overlap of suitable areas for both species was initially high and then declined in the current period and future epochs in the RCP 2.6 scenario, but increased in the RCP 8.5 scenario. In short, the responses of both *Ficus* species to climate change differed. Thus, specific actions such as ex situ conservation and assisted migration may be needed to conserve both species.

Keywords: ecological niche model; Indo-Burma; sympatric species; habitat suitability; MaxEnt



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1. Introduction

Global climate change poses a serious threat to natural ecosystems and biodiversity in tropical and temperate climate zones [1–3]. Habitat loss and fragmentation due to anthropogenic disturbance and activities can also impact biodiversity and isolation of geographic areas [4–7]. Ecological niche models (ENMs) can be used to investigate the effects of environmental change on the species distributions across extended timescales, using sampling occurrence and the environmental factors to predict the potential habitats of species. Moreover, the ENMs can more accurately predict species distributions when they incorporate information on population genetic structure and, concomitantly, local adaptation [8,9]. Under changing climates, species generally respond by adaptation or extinction, with 15–37% of species predicted to go extinct by 2050 [10–12]. Hence, conservation strategies are critical for slowing the rate of species loss [11].

The Indo-Burma region is a hotspot of geographic diversity, covering southern China, Laos, Myanmar, Vietnam, Cambodia, and Thailand. The region supports a variety of habitats spanning 0–6000 m in elevation and experiences strong seasonal climates. Notably,

in summer, the southern and western parts are dominated by the southwest monsoon and the northeastern part is dominated by the northeast monsoon, with drier conditions prevailing throughout much of the region in winter [13]. The region supports 15,000–25,000 species of flora and more than 2000 species of fauna [14–16], and new species continue to be discovered. Under the influence of climate change, it is predicted that 1.9–40.5% of endemic plant and vertebrate species in this region will go extinct over the next century [17].

Of the approximately 800 *Ficus* species recognized worldwide, most are distributed in tropical regions. Fig trees provide nutrients, microclimates, and predator protection for the organisms living within them (e.g., pollinator and parasitic wasps, ants, mites, and nematodes) [18]. Fig trees and pollinating fig wasps (Agonidae) exhibit species-specific mutualistic relationships, with one *Ficus* species allowing one specific agonid species to enter the syconium to complete pollination [19–21]. However, several recent studies have reported a breakdown of the one-to-one rule in the fig–fig wasp breeding system, whereby one *Ficus* species is pollinated by more than one fig wasp species, or two *Ficus* species could share the same pollinator [22–27]. For example, the closely related dioecious *Ficus squamosa* and *Ficus heterostyla* share a pollinating fig wasp species in overlapping distribution areas of the Indo-Burma region [28,29], despite different habitats. *Ficus squamosa* is a small riparian shrub species. Its figs grow along branches close to the ground, which are often submerged during the rainy season, and seeds are primarily dispersed by water [30]. In contrast, *F. heterostyla* is a small deciduous species [31] that grows in forest, secondary forest, and along roadsides. Its figs are located in rooting stolons near or under the soil, where soil moisture and temperature influence fruit development. Both *Ficus* species show complementary fruiting phenologies in the Xishuangbanna region, which facilitates the sharing of a single pollinator fig wasp species [28]. Ecological niche overlap of the two sympatric *Ficus* species and the change in potential distribution under climate change are worth studying to better understand fig and fig wasp mutualism.

In recent years, maximum entropy model (MaxEnt) software has been widely used to understand fluctuations in the distribution of species impacted by climate change [32–36]. In this study, MaxEnt was used to model habitat suitability of the two sympatric *Ficus* species in the Indo-Burma region. We aimed to answer the following questions: (1) What are the suitable distribution ranges of both species under the current environment? (2) How has species distribution changed since the Last Glacial Maximum (LGM), and how will habitat availability change in the future (2050 and 2070)? (3) Does suitable habitat overlap between the two species?

2. Materials and Methods

2.1. Study Area and Collection of Species Occurrence Data

Ficus squamosa Roxb. (Subgenus *Sycomorus*, Section *Sycocarpus*) is distributed in Nepal, Bhutan, Sikkim, north-east India, Myanmar, Laos, and China (Yunnan), while *F. heterostyla* Merr. (Subgenus *Sycomorus*, Section *Hemicardia*) is distributed in Thailand, Vietnam, Laos, and Cambodia [37]. Both *Ficus* species show overlapping distributions in the Xishuangbanna region of China and share an undescribed pollinating fig wasp (*Ceratosolen* sp.) [28]. From 2008 to 2018, we conducted several field surveys and sample collections in China, Laos, Myanmar, Vietnam, Cambodia, and Thailand (98.5° E–109.5° E and 9.5° N–26.5° N). We investigated the distributions of both species referring to the Flora of Thailand [37] and Flora of China [38], as well as other potential parts of their ranges. We recorded 143 occurrences for *F. squamosa* and 257 occurrences of *F. heterostyla* in natural conditions, during April of 2008, April of 2014, and February of 2018 in China, June of 2013 in Vietnam, April of 2015 in Cambodia, October of 2016 in Myanmar, January of 2012, July of 2013, August of 2014, and March and October of 2018 in Thailand, and October of 2018 in Laos. We also downloaded the distribution data of both species from the Global Biodiversity Information Facility (GBIF) website (<https://doi.org/10.15468/dl.m8cqz7>, accessed on 21 August 2022), including 16 records for *F. squamosa* and nine records for *F. heterostyla*. All data obtained were exported to ArcGIS v10.5, with and duplicate presence data within

1 km removed, involving 104 points for *F. squamosa* and 199 points for *F. heterostyla*. Finally, the distribution data of the two sympatric species included 55 records of *F. squamosa* and 67 records of *F. heterostyla* (the source and distribution of all records are provided in Figure 1 and Table S1 in Supplementary Materials). We retained these records to match climate variables for further model analysis.

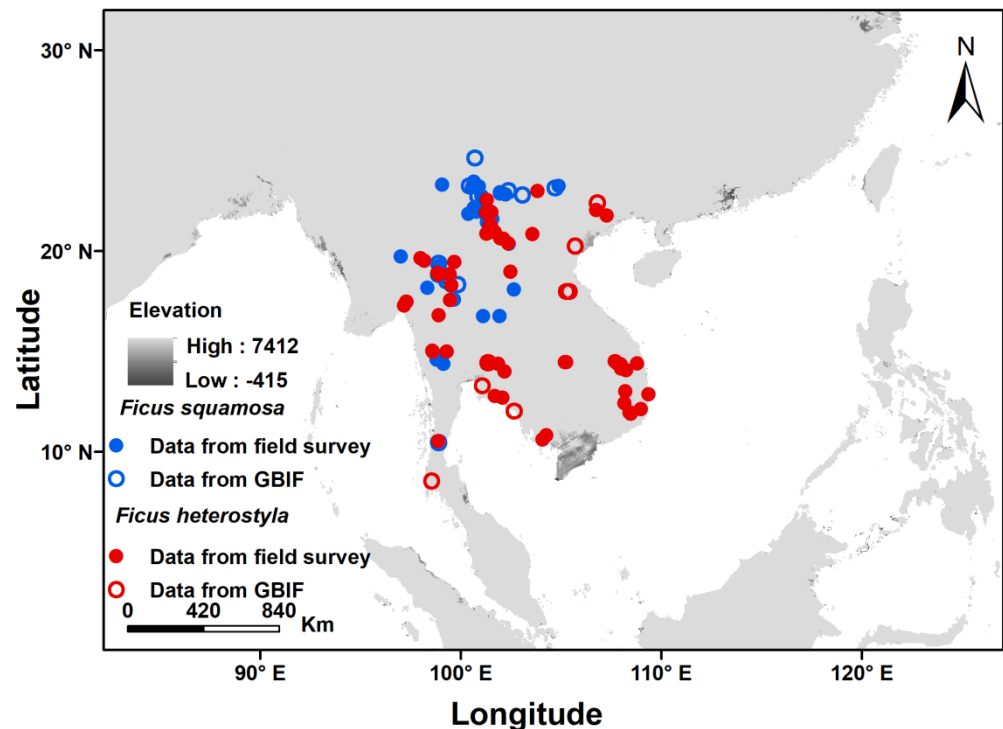


Figure 1. Study area covering habitat of *F. squamosa* and *F. heterostyla*.

2.2. Environmental Variables

Before modeling species distributions, we tried to consider the variables that impacted on species distributions and could limit distributions at key periods. To model the habitat of target species, 19 bioclimatic and 13 other environmental variables were obtained from WorldClim (<http://www.worldclim.org/>, accessed on 21 August 2022), soilgrids250, and Global Forest Change [39]. To encompass forest cover (also important for seed dispersers), we included two parameters, tree height [40] and canopy cover [41]. These variables included 11 soil variables, forest canopy, and forest cover at 30 s resolution. Pearson correlation analysis was performed on the 19 bioclimatic variables at a threshold of 0.85 to exclude highly correlated variables. However, we tried to retain at least a maximum, minimum, mean/annual, and seasonality variable for both temperature and precipitation to determine limiting factors across the year. Using this criterion, nine bioclimatic variables and seven other environmental variables were selected to generate the model (Table 1). Elevation, whilst a useful variable for contemporary analysis, cannot be used for analysis over extended timescales, as it is a correlate of climate and not a direct driver, and using it for projective analysis would preclude the ability of projections to track climate across altitudes (as whilst their climate zone may shift upslope, a model using elevation as a direct driver would limit this shift). This would artificially limit species projections over time. This means that elevation would bias models of future movement, by restricting the ability of species to track climate, as well as falsely truncating species climate niches due to clearance of habitat at lower elevational bands. Furthermore paleo-elevation is notoriously challenging and risks introducing artifacts into analysis, especially in hindcast analysis, which would be hard to particularly capture across the then emergent Sunda shelf. Thus, different variables were used for contemporary and temporal analysis.

Table 1. Environmental variables selected for modeling.

Category	Variable	Abbreviation	Source
Soil variables	Bulk density *	bdod *	SoilGrids250m
	Cation exchange capacity (at pH 7)	cec	
	Coarse fragments	cfvo	
	Clay content *	clay *	
	Nitrogen	nitrogen	
	Organic carbon density *	ocd *	
	Soil organic carbon stock	ocs	
	Soil pH	ph	
	Sand *	sand *	
	Silt *	silt *	
Habitat variables	Soil organic carbon	soc	[40,41]
	Tree height *	canopy *	
Bioclimatic variables	Forest cover	cover	WORLDCLIM
	Annual mean temperature *	bio1 *	
	Mean diurnal range (mean of monthly (max temp – min temp))	bio2	
	Isothermality (BIO2/BIO7) ($\times 100$)	bio3	
	Temperature seasonality (standard deviation $\times 100$)	bio4	
	Max temperature of warmest month *	bio5 *	
	Min temperature of coldest month *	bio6 *	
	Temperature annual range (BIO5–BIO6)	bio7	
	Mean temperature of wettest quarter	bio8	
	Mean temperature of driest quarter	bio9	
	Mean temperature of warmest quarter *	bio10 *	
	Mean temperature of coldest quarter *	bio11 *	
	Annual precipitation	bio12	
	Precipitation of wettest month *	bio13 *	
	Precipitation of driest month *	bio14 *	
	Precipitation seasonality (coefficient of variation)	bio15	
	Precipitation of wettest quarter *	bio16 *	
	Precipitation of driest quarter	bio17	
	Precipitation of warmest quarter	bio18 *	
	Precipitation of coldest quarter *	bio19 *	

* Variables excluded in final model simulation.

The LGM and Mid-Holocene warm period (Mid-Hol) were predicted using the nine selected bioclimatic variables (based on the assessment for redundancy detailed below) using the calibrated global climate model (GCM) data based on the Community Climate System Model ‘CCSM4’, while current and future periods (2050 and 2070 in the RCP 2.6 and RCP 8.5 scenario) were predicted with 16 (current) and 15 (future) environmental variables. The mask was created for the last glacial maximum by calculating exposed land for that period, using a bathymetric layer, and calculating the land exposed by subtracting 111 m and then classifying the area still above that level [42]. The future periods included Representative Concentration Pathway 2.6 (RCP 2.6) and Representative Concentration Pathway 8.5 (RCP 8.5) to represent both optimistic and pessimistic scenarios [43]. We used the default settings in MaxEnt, with fivefold replicates with bootstrap validation; we then used the average of the five models. Final model outputs were exported and analyzed in ArcGIS v. 10.5 (ESRI, Redlands, CA, USA).

2.3. Ecological Niche Model

MaxEnt v-3.4.0 [44] was used to model changing distributions of the species from the Last Glacial Maximum (LGM) to 2070 including two different scenarios. Spatial rarefaction of localities was performed using the buffer and intersect in ArcGIS to reduce autocorrelation between the points at each grid cell (size 1×1 km). Removal of clustered points left 122 locations which were retained and used for subsequent analyses. Overlap between sites of both species was evaluated using the indices of equivalence (D) and similarity (I)

according to the tests proposed by Warren et al. [45]. In ecology, Schoener's index (D) is used to evaluate ecological niche and microhabitat overlap, while Hellinger's index (I) is derived from distance, based on the comparison of probability distributions. Both indices range from 0 (no overlap) to 1 (models are identical). The potential habitats in 2050 and 2070 were determined to evaluate the future risk of species status [46].

3. Results

3.1. Model Performance

According to Pearson correlation analysis, nine of the 19 bioclimatic variables were significant for constructing the ENMs for *F. squamosa* and *F. heterostyla*. The models were validated using AUC values, with all models showing an AUC >0.9, thus being considered excellent [47]. Following these criteria, all habitat suitability models of *F. squamosa* and *F. heterostyla* were excellent. In the current period MaxEnt model, the Boyce index for *F. squamosa* and *F. heterostyla* was 0.842 and 0.875, respectively. For the 2050 and 2070 prediction models, the Boyce index for *F. squamosa* and *F. heterostyla* in different emission scenario was greater than 0.8 (Table S2).

3.2. Environmental Variable Importance

According to variable importance, both species had specific areas of suitable habitats based on percentage contribution and permutation importance estimated by MaxEnt (Table 2). The jackknife test for regularized training gain indicated that temperature seasonality (Bio4) and isothermality (Bio3) showed the highest contribution to the prediction of suitable habitats for *F. squamosa* and *F. heterostyla* (Figure S1). Interestingly, other variables contributing to the prediction of suitable habitat included mean diurnal range (Bio2) and cation exchange capacity (at pH 7) for *F. squamosa* and precipitation of driest quarter (Bio17) for *F. heterostyla* (Table 2).

Table 2. Percentage contribution and permutation importance of environmental variables in predicting species distribution.

Abbreviation	Variable Definition	<i>Ficus squamosa</i>		<i>Ficus heterostyla</i>	
		Contribution (%)	Permutation	Contribution (%)	Permutation
cec	Cation exchange capacity (at pH 7)	10.9	13.4	1.3	1.3
cfvo	Coarse fragments	4.9	3	3.1	2.4
nitrogen	Nitrogen	0.2	0.5	4.8	4.7
ocs	Soil organic carbon stock	0.7	3.5	1.3	2.2
ph	Soil pH	3.5	2.9	1	0.7
soc	Soil organic carbon	0.8	0.9	1.9	1.4
cover	Forest cover	0.3	0.6	7.3	3.8
bio2	Mean diurnal range (mean of monthly (max temp – min temp))	33.9	40.5	1.2	1.6
bio3	Isothermality (BIO2/BIO7) ($\times 100$)	17.4	0	7.6	1
bio4	Temperature seasonality (standard deviation $\times 100$)	5.4	9.6	23.6	40.9
bio7	Temperature annual range (BIO5–BIO6)	5.3	0.5	17.8	0.6
bio8	Mean temperature of wettest quarter	3.2	4.2	0.1	0.8
bio9	Mean temperature of driest quarter	1.3	1.9	3.9	0.6
bio12	Annual precipitation	2.8	11	0.3	0.1
bio15	Precipitation seasonality (coefficient of variation)	3.6	2.2	8.9	0.7
bio17	Precipitation of driest quarter	5.8	5.4	15.8	37.5

Note: Variables with more than 5% contribution and permutation are highlighted in **bold**.

The bioclimatic ranges of nine variables for both species are shown in Table 3, showing that drivers varied between species; *F. heterostyla* could tolerate higher daily tempera-

ture fluctuations than *F. squamosa*, which was distributed in areas with smaller annual temperature fluctuations.

Table 3. Bioclimatic ranges for *F. squamosa* and *F. heterostyla*. Key factors are noted in **bold**.

Environmental Variable	<i>F. squamosa</i>		<i>F. heterostyla</i>	
	Suitable Ranges	Most Suitable Value	Suitable Ranges	Most Suitable Value
Mean diurnal range (°C)	>9.69	12.04	>3.53	12.04
Isothermality	43.47–74.97	51.48	46.97–78.92	58.40
Temperature seasonality (C of V)	10.29–48.82	24.68	6.24–37.58	14.56
Temperature annual range (°C)	14.56–27.50	21.99	9.92–23.43	15.30
Mean temperature of wettest quarter (°C)	14.29–29.43	25.64	>18.85	25.86
Mean temperature of driest quarter (°C)	3.90–28.46	22.07	>15.05	21.70
Annual precipitation (mm)	<2525.67	1 129.60	>905.74	\
Precipitation seasonality (C of V)	0.49–1.19	0.78	0.57–1.22	0.76
Precipitation of driest quarter (mm)	8.06–161.52	37.06	20.46–132.17	37.65

3.3. Predicting Suitable Habitats

Past, current, and future predictions of suitable habitat for *F. squamosa* and *F. heterostyla* are shown in Figures 2 and 3, respectively. The ten-percentile training presence cog-log threshold was used to delineate unsuitable from suitable habitats. The distribution of suitable habitat for both species in the current period was considerably higher than known occurrences, as indicated by collected data and existing records.

During the LGM, both species had larger distribution areas than during the Mid-Hol and current period, as large portions of the now submerged Sunda shelf were suitable. Future projections for 2050 and 2070 suggested that regions from southern China to northern Thailand would still exhibit high habitat suitability potential for *F. squamosa* and *F. heterostyla*, but habitat suitability for both species would reduce overall across the whole study area, although some expansions may occur in 2070.

3.4. Niche Overlap and Distribution Area for Both Species

For the two species, the niche overlap of suitable areas was initially high and then declined in the current period and future epochs in they RCP 2.6 scenario, but they increased in the RCP 8.5 scenario, exceeding that under RCP 2.6 (Table 4, Figure 4). Suitable habitats for both species were found in southern China and Southeast Asia in the different time periods, with the overlapping area decreasing in the RCP 2.6 scenario and increasing in RCP 8.5 scenario (Table 5).

Table 4. Ecological niche overlap of suitable habitat between *F. squamosa* and *F. heterostyla* in current, RCP 2.6 2050, RCP 2.6 2070, RCP 8.5 2050, and RCP 8.5 2070 periods, as indicated by equivalence (*D*) and similarity (*I*) parameters.

Niche Overlap	Schoener's Parameter (<i>D</i>)	Hellinger's-Based Parameter (<i>I</i>)
Current epoch	0.7030	0.9253
RCP2.6 2050	0.7168	0.9332
RCP2.6 2070	0.6979	0.9259
RCP8.5 2050	0.7336	0.9376
RCP8.5 2070	0.7941	0.9625

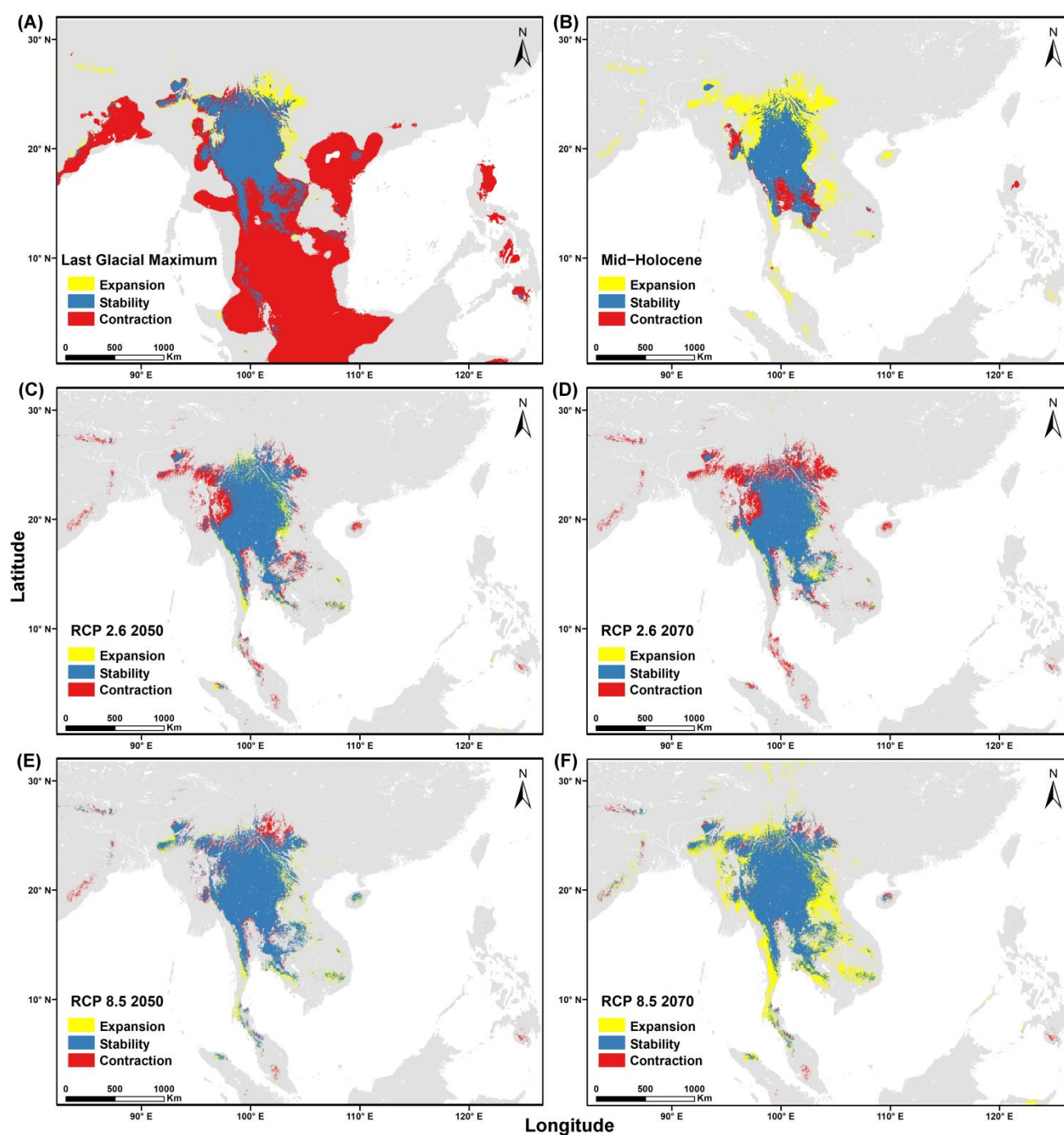


Figure 2. From past to current (red areas indicate areas previously suitable and lost by the present period) and from current to future (red areas indicate areas currently suitable which will be lost), the expanded and contracted range of *F. squamosa*. (A) Last Glacial Maximum (LGM), (B) Mid-Holocene, (C) future (RCP 2.6 2050), (D) future (RCP 2.6 2070), (E) future (RCP 8.5 2050), and (F) future (RCP 8.5 2070).

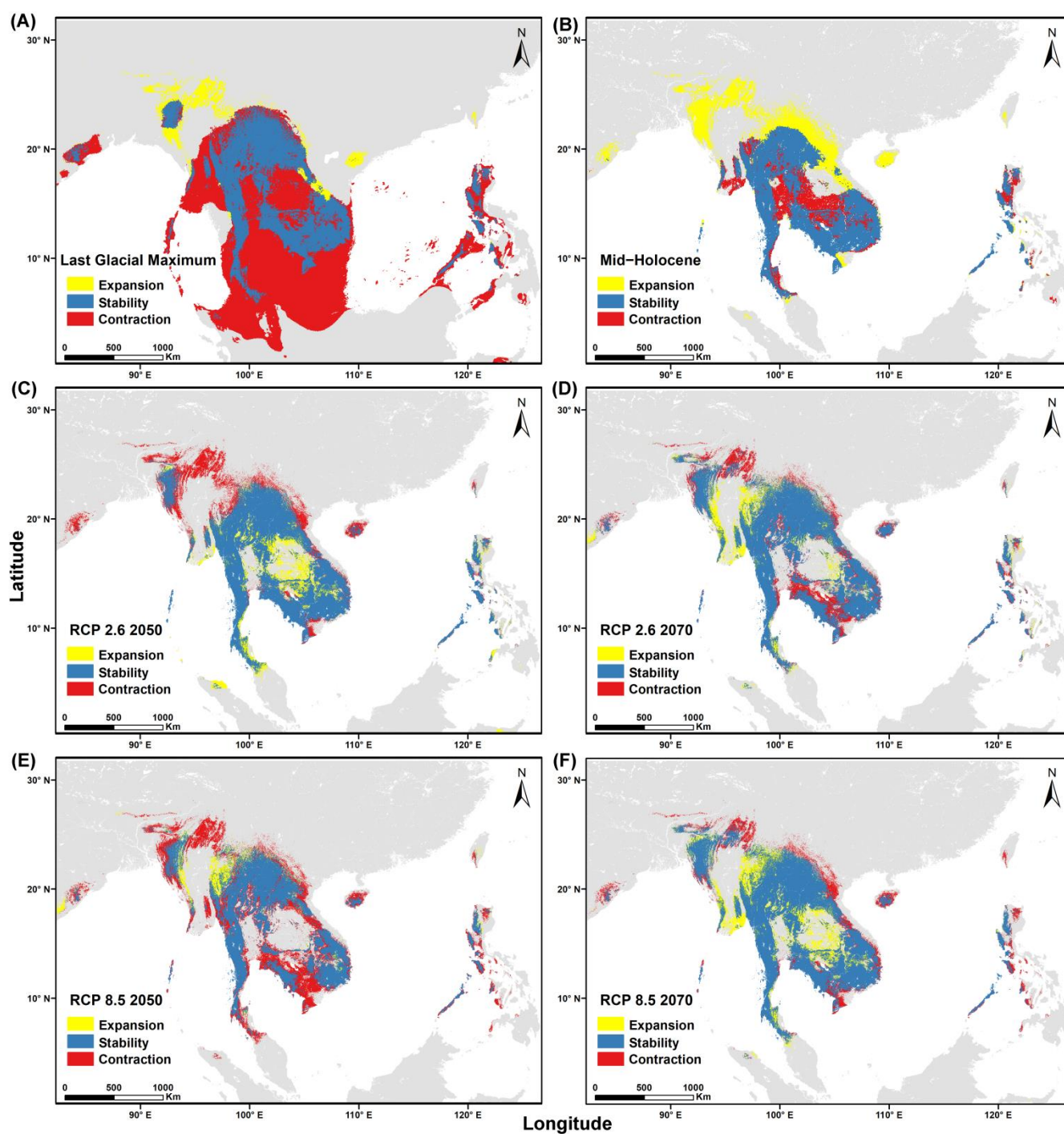


Figure 3. From past to current (red areas indicate areas previously suitable and lost by the present period) and from current to future (red areas indicate areas currently suitable which will be lost), the expanded and contracted range of *F. heterostyla*. (A) Last Glacial Maximum (LGM), (B) Mid-Holocene, (C) future (RCP 2.6 2050), (D) future (RCP 2.6 2070), (E) future (RCP 8.5 2050), and (F) future (RCP 8.5 2070).

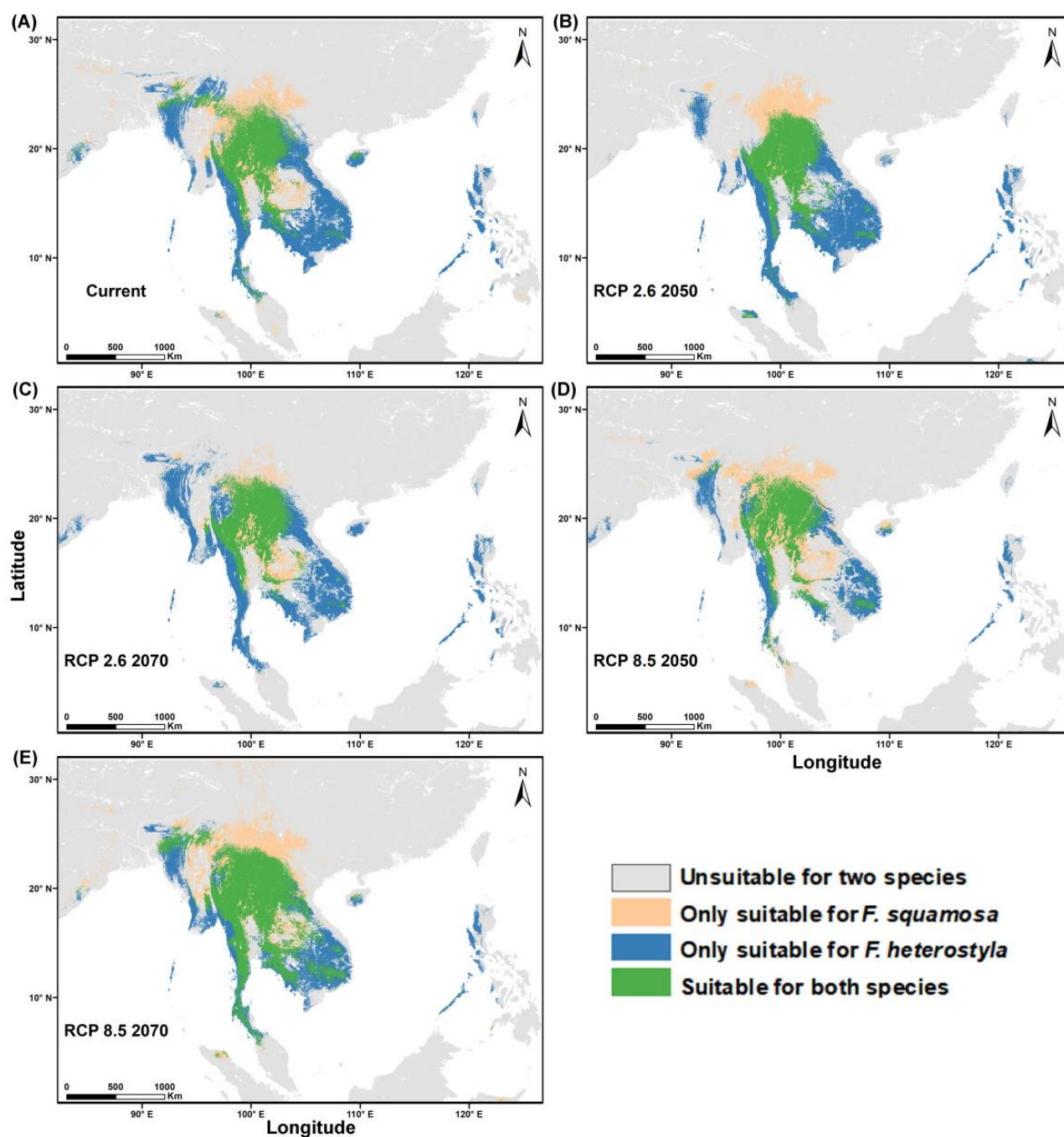


Figure 4. Overlapping maps of *F. squamosa* and *F. heterostyla* for current period and future. Gray refers to unsuitable areas for both species; yellow refers to areas only suitable for *F. squamosa*; blue refers to areas only suitable for *F. heterostyla*; green refers to areas suitable for both species. (A) Current, (B) future (RCP 2.6 2050), (C) future (RCP 2.6 2070), (D) future (RCP 8.5 2050), and (E) future (RCP 8.5 2070).

Table 5. The percentage of suitable habitats in the study area for *F. squamosa* and *F. heterostyla* in different periods.

Species	Area (%)						
	LGM	Mid	Current	RCP 2.6 2050	RCP 2.6 2070	RCP 8.5 2050	RCP 8.5 2070
<i>F. squamosa</i>	31.76%	7.80%	12.49%	10.28%	9.10%	12.34%	17.69%
<i>F. heterostyla</i>	29.97%	16.54%	18.91%	17.37%	17.49%	12.71%	19.11%
Overlap	N.D.	N.D.	7.57%	7.09%	6.43%	6.55%	12.05%

4. Discussion

In this study, ENMs were used to accurately predict the habitat suitability of two *Ficus* species [48]. On the basis of climatic variables, the MaxEnt model indicated that the distribution of both species has declined from past to current. The predicted future distributions exhibit high habitat suitability potential for *F. squamosa* and *F. heterostyla*, from southern China to northern Thailand, but habitat suitability for both species would reduce overall across the whole study area, although some expansions may occur in 2070. The seed dispersal would be key for this expansion to occur (which with the loss of larger bodied fruitbats due to hunting may be improbable). The two species showed considerable overlap in suitable habitat, which would decrease in the future. These results are consistent with the changes in area percentage for *F. squamosa* and the potential of *F. heterostyla* to better adapt to the changing environments [49], confirming that different species can detect changes in the climate and respond differently [50]. The two species showed large overlap in suitable area in the current model, indicating that they coexist in a large area. How do these coexisting species avoid competition? One explanation is their preference for different microhabitats, i.e., *F. squamosa* is a riparian species while *F. heterostyla* grows in forest, secondary forest, and along roadsides. In addition, a short overlap in flowering time, which reflects the timing of specific resource requirements by plants, in coexisting species may reduce competition for pollinator resources [51]. The primary region of overlapping distribution for both species is located toward the northern edge of tropical Asia with a highly seasonal climate. In response to seasonality, both *Ficus* species exhibit complementary flowering phenologies to facilitate the sharing of a single pollinator fig wasp species [28], thus supporting the temporal niche partitioning in the coexistence of plant species in the community. Previous studies have reported that climate change will affect the patterns of precipitation and temperature, especially in lowland ecosystems [52–55], with warmer surface water in concert with higher air temperatures [55]. Temperature (Bio4, Bio3) may have a stronger influence on the lowland species *F. squamosa*. In addition, for forest-distributed *F. heterostyla*, precipitation of the driest quarter (Bio17) may also significantly affect suitable niche range.

Previous research found that the 11 sympatric species of *Zaluzania* in Mexico show low values of overlap, suggesting that the species evolved in divergent environments [49]. However, our results indicated a high percentage of niche interactions between the sympatric species, with both influenced by similar variables, including temperature (Bio4, Bio3) and elevation. Notably, *F. heterostyla* can tolerate higher daily temperature fluctuations than *F. squamosa*, which is distributed in areas with smaller annual temperature fluctuations, and this may enable to allow the two species to co-exist [56,57]. In species-specific fig–fig wasp mutualism, pollinating fig wasps will influence the distribution of *Ficus* hosts, and those with short life cycles may be more sensitive to climate change. Thus, the response and adaptation of fig–fig wasp mutualism to climate change deserve further study.

The two species continue to overlap for both *Ficus* species in the past, current, and future (next five decades). These results suggest that *F. heterostyla* and *F. squamosa* will continue to coexist in the same areas as long as their shared pollinator can also survive in the region. Volatile organic compounds (VOCs) released by receptive figs play crucial roles in attracting pollinators and are sensitive to climate change [58]; thus, they are worthy of further study. Our results suggested that the distribution range of the two *Ficus* species is narrow and influenced by specific variables, facilitating targeted conservation efforts [59–62].

5. Conclusions

Both *F. squamosa* and *F. heterostyla* are distributed along the northern edge of tropical Asia, with the high seasonality in Xishuangbanna leading to the sharing of a single pollinator species. Both *Ficus* species are predominantly influenced by temperature and isothermality. In the future, the potential suitable distribution area of *F. squamosa* will decrease, while that of *F. heterostyla* will increase slightly but become increasingly fragmented. The niche overlap of suitable habitat of both species was high but decreased in the

future. Both *Ficus* species show large responses to climate change, but their survival will be dependent on the presence of pollinating fig wasps and negatively impacted by human disturbance, while expansions may be contingent on the spread of fruit via vertebrate species which are also threatened.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/f13091420/s1>: Table S1. The occurrence data of *Ficus squamosa* and *Ficus heterostyla* used for the ENM analysis; Table S2. Predictive performance of ensemble ENMs for *F. squamosa* and *F. heterostyla*; Figure S1. Jackknife test for regularized training gain of environmental variable importance for (A) *F. squamosa* and (B) *F. heterostyla*; blue bars are relative to all environmental variables; the red bar indicates the MaxEnt model.

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Conflicts of Interest: The authors declare no conflict of interest.

References

1. Jump, A.S.; Peñuelas, J. Genetic effects of chronic habitat fragmentation in a wind-pollinated tree. *Proc. Natl. Acad. Sci. USA* **2006**, *103*, 8096–8100. [CrossRef] [PubMed]
2. Thornton, P.K.; Herrero, M.; Freeman, H.A.; Okeyo, A.M.; Rege, E.; Jones, P.G.; McDermott, J. Vulnerability, climate change and livestock-opportunities and challenges for the poor. *J. Semi-Arid. Trop. Agric. Res.* **2007**, *4*, 1–23.
3. Bacles, C.F.E.; Jump, A.S. Taking a tree's perspective on forest fragmentation genetic. *Trends Plant Sci.* **2011**, *16*, 13–18. [CrossRef]
4. Garcia-Valdés, R.; Svennig, J.-C.; Zavala, M.A.; Purves, D.W.; Araújo, M.B. Evaluating the combined effects of climate and land-use change on tree species distribution. *J. Appl. Ecol.* **2015**, *52*, 902–912. [CrossRef]
5. Zambrano, J.; Garzon-Lopez, C.X.; Yeager, L.; Fortunel, C.; Cordeiro, N.J.; Beckman, N.G. The effects of habitat loss and fragmentation on plant functional traits and functional diversity: What do we know so far? *Oecologia* **2019**, *191*, 505–518. [CrossRef] [PubMed]
6. Zhang, C.; Xai, W.; Luan, X.; Zhuang, H.; Khan, T.U.; Zhang, G.; Wu, S. Use of historical data to assess the impact of climate change and anthropogenic disturbance on the black-billed capercaillie (*Tetrao urogalloides*) in northeast China. *Glob. Ecol. Conserv.* **2020**, *22*, e00972. [CrossRef]
7. Dibattista, J.D. Patterns of genetic variation in anthropogenically impacted populations. *Conserv. Genet.* **2008**, *9*, 141–156. [CrossRef]
8. Ikeda, D.; Max, T.L.; Allan, G.J.; Lau, M.K.; Shuster, S.M.; Whitham, T.G. Genetically informed ecological niche models improve climate change predictions. *Glob. Chang. Biol.* **2017**, *23*, 164–176. [CrossRef]
9. Culshaw, V.; Mairal, M.; Sanmartin, I. Biogeography meets niche modeling: Interring the role of deep time climate change when data is limited. *Front. Ecol. Evol.* **2021**, *9*, 662092. [CrossRef]
10. Williams, J.E. The biodiversity crisis and adaptation to climate change: A case study from Australia's forests. *Environ. Monit. Assess.* **2000**, *61*, 65–74. [CrossRef]
11. Lewis, O.T. Climate change, species-area curves and the extinction crisis. *R. Soc.* **2006**, *361*, 1465. [CrossRef] [PubMed]
12. Rinawati, F.; Stein, K.; Lindner, A. Climate change impacts on biodiversity—the setting of a lingering global crisis. *Diversity* **2013**, *5*, 114–123. [CrossRef]
13. Tordoff, A.W.; Bezuijen, M.R.; Duckworth, J.W.; Fellowes, J.R.; Koenig, K.; Pollard, E.H.B.; Royo, A.G. *Ecosystem Profile Indo-Burma Biodiversity Hotspot 2011 Update*; Critical Ecosystem Partnership Fund: Washington, DC, USA, 2012.
14. Davis, S.D.; Droop, S.J.; Gregerson, P.; Henson, L.; Leon, C.J.; Synge, H.; Villa-Lobos, J.L.; Zantovska, J. *Plants in Danger, What Do We Know*; IUCN: Gland, Switzerland; Cambridge, UK, 1986.

15. Davis, S.D.; Heywood, V.H.; Hamilton, A.C. *Centres of Plant Diversity: A Guide and Strategy for Their Conservation: Asia, Australasia and the Pacific*; IUCN Publications Unit: Cambridge, UK, 1995; Volume 2.
16. Mittermeier, R.A.; Robles Gil, P.; Hoffmann, M.; Pilgrim, J.D.; Brooks, T.M.; Mittermeier, C.G.; Lamoreux, J.; da Fonseca, G.A.B. *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Ecoregions*; CEMEX: Mexico City, Mexico, 2004.
17. Malcolm, J.R.; Liu, C.; Neilson, R.P.; Hansen, L.; Hannah, L. Global warming and extinctions of endemic species from biodiversity hotspots. *Conserv. Biol.* **2006**, *20*, 538–548. [[CrossRef](#)] [[PubMed](#)]
18. Herre, E.; Jandér, K.; Machado, C. Evolutionary ecology of figs and their associates: Recent progress and outstanding puzzles. *Annu. Rev. Ecol. Evol. Syst.* **2008**, *39*, 439–458. [[CrossRef](#)]
19. Jenzen, D.H. How to be a Fig. *Annu. Rev. Ecol. Evol. Syst.* **1979**, *10*, 13–51. [[CrossRef](#)]
20. Wiebes, J.T. Co-evolution of figs and their insect pollinators. *Annu. Rev. Ecol. Evol. Syst.* **1979**, *10*, 1–12. [[CrossRef](#)]
21. Cruaud, A.; Rønsted, N.; Chantarasuwan, B.; Chou, L.S.; Clement, W.L.; Couloux, A.; Cousins, B.; Genson, G.; Harrison, R.H.; Hanson, P.E.; et al. An extreme case of plant-insect co-diversification: Figs and fig-pollinating wasps. *Syst. Biol.* **2012**, *61*, 1029–1047. [[CrossRef](#)]
22. Michaloud, G.; Carriere, S.; Kobbi, M. Exceptions to the one: One relationship between African fig trees and their fig wasp pollinators: Possible evolutionary scenarios. *J. Biogeogr.* **1996**, *23*, 513–520. [[CrossRef](#)]
23. Rasplus, J.Y. The one-to-one species-specificity of the Ficus-Agaoninae mutualism: How casual? In *The Biodiversity of African Plants*; van der Maesen, L.J.G., van der Burgt, X.M., van Medenbach de Rooy, J.M., Eds.; Kluwer Academic Publishers: Wageningen, The Netherlands, 1996; pp. 639–649.
24. Moe, A.M.; Rossi, D.R.; Weiblen, G.D. Pollinator sharing in dioecious figs (*Ficus*: Moraceae). *Biol. J. Linn. Soc.* **2011**, *103*, 546–558. [[CrossRef](#)]
25. Darwell, C.T.; Al-Beidh, S.; Cook, J.M. Molecular species delimitation of a symbiotic fig-pollinating wasp species complex reveals extreme deviation from reciprocal partner specificity. *BMC Evol. Biol.* **2014**, *14*, 189. [[CrossRef](#)]
26. Yu, H.; Tian, E.; Zheng, L.; Deng, X.; Cheng, Y.; Chen, L.; Wu, W.; Tanming, W.; Zhang, D.; Compton, S.G.; et al. Multiple parapatric pollinators have radiated across a continental fig tree displaying clinal genetic variation. *Mol. Ecol.* **2019**, *28*, 2391–2405. [[CrossRef](#)] [[PubMed](#)]
27. Zhang, T.; Jandér, K.C.; Huang, J.F.; Wang, B.; Zhao, J.B.; Miao, B.G.; Peng, Y.Q.; Herre, E.A. The evolution of parasitism from mutualism in wasps pollinating the fig, *Ficus microcarpa*, in Yunnan Province, China. *Proc. Natl. Acad. Sci. USA* **2021**, *188*, e2021148118. [[CrossRef](#)] [[PubMed](#)]
28. Liu, G.X.; Yang, D.R.; Peng, Y.Q.; Compton, S.G. Complementary fruiting phenologies facilitate sharing of one pollinator fig wasps by two fig trees. *J. Plant Ecol.* **2015**, *8*, 197–206. [[CrossRef](#)]
29. Fungjanthuek, J.; Zhang, Z.R.; Peng, Y.Q.; Gao, J. The complete chloroplast genome of two related fig species *Ficus squamosa* and *Ficus heterostyla*. *Mitochondrial DNA Part B* **2022**, *7*, 236–238. [[CrossRef](#)]
30. Pothasin, P.; Compton, S.G.; Wangpakapattanawong, P. Seasonality of leaf and fig production in *Ficus squamosa*, a fig tree with seeds dispersed by water. *PLoS ONE* **2016**, *11*, e0152380. [[CrossRef](#)] [[PubMed](#)]
31. Shanahan, M.; So, S.; Compton, S.G.; Corlett, R.T. Fig-eating by vertebrate frugivores: A global review. *Biol. Rev.* **2001**, *76*, 529–572. [[CrossRef](#)]
32. Stock, C.A.; Alexander, M.A.; Bond, N.A.; Brander, K.M.; Cheung, W.W.; Curchitser, E.N.; Delworth, T.L.; Dunne, J.P.; Griffies, S.M.; Haltuch, M.A.; et al. On the use of IPCC-class models to assess the impact of climate on living marine resources. *Prog. Oceanogr.* **2011**, *88*, 1–27. [[CrossRef](#)]
33. Bojinski, S.; Verstraete, M.; Peterson, T.C.; Richter, C.; Simmons, A.; Zemp, M. The concept of essential climate variables in support of climate research, applications, and policy. *Bull. Am. Meteorol. Soc.* **2014**, *95*, 1431–1443. [[CrossRef](#)]
34. Harris, R.M.B.; Grose, M.R.; Lee, G.; Bindoff, N.L.; Porfiro, L.L.; Fox-Hughes, P. Climate projections for ecologists: Climate projections for ecologists. *Wiley Interdiscip. Rev. Clim. Chang.* **2014**, *5*, 621–637. [[CrossRef](#)]
35. Cavanagh, R.D.; Murphy, E.J.; Bracegirdle, T.J.; John, T.; Knowland, C.A.; Corney, S.P.; Smith, W.O.; Waluda, C.M.; Johnston, N.M.; Bellberby, R.G.J. A synergistic approach for evaluating climate model output for ecological applications. *Front. Mar. Sci.* **2017**, *4*, 308. [[CrossRef](#)]
36. Li, Y.; Li, M.; Li, C.; Liu, Z. Optimized Maxent model predictions of climate change impacts on the suitable distribution of *Cunninghamia lanceolata* in China. *Forests* **2020**, *11*, 302. [[CrossRef](#)]
37. Berg, C.C.; Pattharahirantracin, N.; Chantarasuwan, B. Cecropiaceae and Moraceae. In *Flora of Thailand*; Santisuk, T., Larsen, K., Eds.; Forest Herbarium, Royal Forest Department: New York, NY, USA, 2011; Volume 10, pp. 475–675.
38. Zhou, Z.; Gilbert, M.G. Flora of China. 2003, 5, 37–71. Available online: http://www.efloras.org/flora_page.aspx?flora_id=2 (accessed on 21 August 2022).
39. Warren, D.L.; Seifert, S.N. Ecological niche modeling in Maxent: The importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* **2011**, *21*, 335–342. [[CrossRef](#)] [[PubMed](#)]
40. Crowther, T.W.; Glick, H.B.; Covey, K.R.; Bettigole, C.; Maynard, D.S.; Thomas, S.M.; Smith, J.R.; Hintler, G.; Duguid, M.C.; Amatulli, G.; et al. Mapping tree density at a global scale. *Nature* **2015**, *525*, 201–205. [[CrossRef](#)]
41. Simard, M.; Pinto, N.; Fisher, J.B.; Baccini, A. Mapping forest canopy height globally with spaceborne lidar. *J. Geophys. Res. Biogeosciences* **2011**, *116*, G04021. [[CrossRef](#)]

42. Hughes, A.C.; Satasook, C.; Bates, P.J.; Bumrungsri, S.; Jones, G. The projected effects of climatic and vegetation changes on the distribution and diversity of Southeast Asian bats. *Glob. Chang. Biol.* **2012**, *18*, 1854–1865. [\[CrossRef\]](#)
43. Meinshausen, M.; Smith, S.J.; Calvin, K.; Daniel, J.S.; Kainuma, M.L.T.; Lamarque, J.F.; Matsumoto, K.; Montzka, S.A.; Raper, S.C.B.; Riahi, K. The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Clim. Chang.* **2011**, *109*, 213–241. [\[CrossRef\]](#)
44. Su, H.; Bista, M.; Li, M. Mapping habitat suitability for Asiatic black bear and red panda in Makalu Barun National Park of Nepal from Maxent and GARP models. *Sci. Rep.* **2021**, *11*, 14135. [\[CrossRef\]](#)
45. Warren, D.L.; Glor, R.E.; Turelli, M. Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution* **2008**, *62*, 2868–2883. [\[CrossRef\]](#)
46. Noce, S.; Caposaso, L.; Santini, M. A new global dataset of bioclimatic indicators. *Sci. Data* **2020**, *7*, 1–12. [\[CrossRef\]](#)
47. Elith, J.; Phillips, S.J.; Hastie, T.; Dudík, M.; Chee, Y.E.; Yates, C.J. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **2011**, *17*, 43–57. [\[CrossRef\]](#)
48. Shao, H.; Tian, J.Q.; Guo, K.; Sun, J.X. Effects of sample size and species traits on performance of Bioclim in predicting geographical distribution of tree species—a case study with 12 deciduous *Quercus* species indigenous to China. *Chin. J. Plant Ecol.* **2009**, *33*, 870–877.
49. Suárez-Mota, M.E.; Villaseñor, J.L. Ecological niche overlap among species of the genus *Zaluzania* (Asteraceae) from the dry regions of Mexico. *Plant Ecol. Evol.* **2020**, *153*, 337–347. [\[CrossRef\]](#)
50. Chown, S.L.; Hoffmann, A.A.; Kristensen, T.N.; Angilletta, M.J.J.; Stenseth, N.C.; Pertaldi, C. Adapting to climate change: A perspective from evolutionary physiology. *Clim. Res.* **2010**, *43*, 3–15. [\[CrossRef\]](#)
51. Jensen, A.M.; Schamp, B.S.; Belleau, A. Evidence of temporal niche separation via low flowering time overlap in an old-field plant community. *Oecologia* **2019**, *189*, 1071–1082. [\[CrossRef\]](#)
52. Seavy, N.E.; Gardali, T.; Golet, G.H.; Griggs, F.O.; Howell, C.A.; Kelsey, R.; Small-Lorenz, S.; Viers, J.H.; Weigand, J. Why climate change makes riparian restoration more important than ever: Recommendations for practice and research. *Ecol. Restor.* **2009**, *27*, 330–338. [\[CrossRef\]](#)
53. Capon, S.J.; Chambers, L.E.; Nally, R.M.; Naiman, R.J.; Davies, P.; Marshall, N.; Pittock, J.; Reid, M.; Capon, T.; Douglas, M.; et al. Riparian ecosystems in the 21st century: Hotspots for climate change adaptation? *Ecosystems* **2013**, *16*, 359–381. [\[CrossRef\]](#)
54. Kominoski, J.S.; Shah, J.J.F.; Canhoto, C.; Fischer, D.G.; Giling, D.P.; González, E.; Griffiths, N.A.; Larránaga, A.; LeRoy, C.J.; Mineau, M.M.; et al. Forecasting functional implications of global changes in riparian plant communities. *Front. Ecol. Environ.* **2013**, *11*, 423–432. [\[CrossRef\]](#)
55. Flanagan, N.E.; Richardson, C.J.; Ho, M. Connecting differential responses of native and invasive riparian plants to climate change and environmental alteration. *Ecol. Appl.* **2015**, *25*, 753–767. [\[CrossRef\]](#)
56. Pearson, R.G.; Dawson, T.P. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **2003**, *12*, 361–371. [\[CrossRef\]](#)
57. Braunisch, L.; Coppes, J.; Arlettaz, R.; Suchant, R.; Schmid, H.; Bollmann, K. Selecting from correlated climate variables: A major source of uncertainty for predicting species distributions under climate change. *Ecography* **2013**, *36*, 971–983. [\[CrossRef\]](#)
58. Proffit, M.; Lapeyre, B.; Buatois, B.; Deng, X.X.; Arnal, P.; Gouzerh, F.; Carrasco, D.; Hossaert-McKey, M. Chemical signal is in the blend: Bases of plant-pollinator encounter in a highly specialized interaction. *Sci. Rep.* **2020**, *10*, 10071. [\[CrossRef\]](#) [\[PubMed\]](#)
59. Qin, A.; Liu, B.; Guo, Q.; Bussmann, R.W.; Ma, F.; Jian, Z.; Xu, G.; Pei, S. Maxent modeling for predicting impacts of climate change on the potential distribution of *Thuja sutchuensis* Franch., an extremely endangered conifer from southwestern China. *Glob. Ecol. Conserv.* **2017**, *10*, 139–146. [\[CrossRef\]](#)
60. Qin, A.; Jin, K.; Batsaikhun, M.E.; Nyamjav, J.; Li, G.; Li, J.; Xue, Y.; Sun, G.; Wu, L.; Indree, T.; et al. Predicting the current and future suitable habitats of the main dietary plants of the Gobi Bear using Maxent modeling. *Glob. Ecol. Conserv.* **2020**, *22*, e01032. [\[CrossRef\]](#)
61. Prayoon, U.; Suksavate, W.; Chaiyes, A.; Winitpornsawan, S.; Tunhikorn, S.; Faengbubpha, K.; Angkaew, C.; Pattanakiat, S.; Duengkae, P. Past, present and future habitat suitable for gaur (*Bos gaurus*) in Thailand. *Agric. Nat. Resour.* **2021**, *55*, 743–756.
62. Valencia-Rodríguez, D.; Jiménez-Segura, L.; Rogéliz, C.A.; Parra, J.L. Ecological niche modeling as an effective tool to predict the distribution of freshwater organisms: The case of the *Sabaleta Brycon henni* (Eigenmann, 1913). *PLoS ONE* **2021**, *16*, e0247876. [\[CrossRef\]](#) [\[PubMed\]](#)