



Predicting the potential distribution of the invasive weed *Mikania micrantha* and its biological control agent *Puccinia spegazzinii* under climate change scenarios in China

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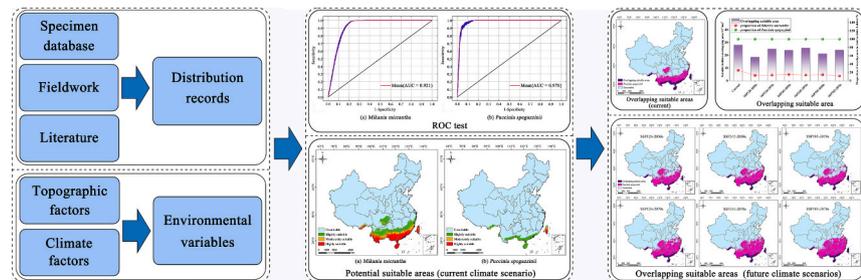
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HIGHLIGHTS

- *Puccinia spegazzinii* shows high potential as a biocontrol agent for *Mikania* vine.
- The potential distribution of *Mikania* and the rust was modelled using MaxEnt.
- The models achieved excellent prediction performance for both species (AUC > 0.92)
- Current climate overlapping suitable areas: *Mikania* (25.2%), *P. spegazzinii* (100%)
- Future climate overlapping suitable areas: *Mikania* (11.6 % – 15.1 %), *P. spegazzinii* (100 %)

GRAPHICAL ABSTRACT



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ABSTRACT

Research on the potential distribution of invasive plants and their biological control agents under climate change is critical for informing strategies in invasive species management. The rust fungus *Puccinia spegazzinii* shows significant potential as a biological control agent for the invasive weed *Mikania micrantha*. The MaxEnt (Maximum Entropy) model was used to simulate the distribution of *M. micrantha* and *P. spegazzinii* under current and future climate scenarios. The models achieved excellent prediction performance, with *M. micrantha* and

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Climate change scenarios
China

P. spegazzinii having area under the curve values of 0.921 and 0.978 respectively, and true skill statistics values of 0.886 and 0.902 respectively. Precipitation is the primary factor influencing the distributions of *M. micrantha*, while *P. spegazzinii* is determined by both temperature and precipitation. The suitable areas for the two species are concentrated in southern China, with *M. micrantha* exhibiting broader adaptability compared to *P. spegazzinii*. Under future climate scenarios, the suitable areas for *M. micrantha* in China will expand northward, with a maximum projected growth rate of 84.6 % in the 2070 s, whereas *P. spegazzinii* exhibits a contracting trend (with a projected reduction of 40.8 % in the 2050 s). Under the current climate scenario, the overlapping suitable areas between the two species account for 25.2 % of the total suitable area for *M. micrantha* and 100 % of that for *P. spegazzinii* and both remain relatively stable under future climate scenarios. This work can provide guidance for the application of biological control, and serves as a valuable reference for developing early warning and management response strategies for invasive species in China.

1. Introduction

Climate change, due to altering temperature patterns and precipitation regimes, and increasing frequency of extreme weather events, may lead to significant changes in the survival, reproduction, and habitats of plant species (Comes and Kadereit, 1998; McCarty, 2001; Kelly and Goulden, 2008). Consequently, both local and global patterns of species distribution are affected, reshaping entire ecosystems (Mooney et al., 2009; Malhi et al., 2020). The ongoing changes in ecosystem structure will further exacerbate the vulnerability of ecosystems, increasing the risk of species extinction, especially in ecologically sensitive regions (Stork et al., 2009; Gao et al., 2022). More critically, climate change and ecosystem disturbances may facilitate the spread of invasive plants that are adapted to unstable and disturbed environments, allowing them to occupy a broader range of habitats (Hellmann et al., 2008; Rahel and Olden, 2008; Bell et al., 2021). This, in turn, poses a significant threat to biodiversity, as invasive species often suppress or even replace native plants, leading to a decline in species richness (Linders et al., 2019; Shen et al., 2024). Invasive species can also impair key ecosystem functions such as nutrient cycling and primary productivity (Thuiller et al., 2005), and can ultimately pose direct threats to human societies, and agriculture and urban environments (Paini et al., 2016; Shackleton et al., 2019).

Mikania micrantha Kunth (Asteraceae), commonly known as mile-a-minute or mikania vine, is a highly invasive climbing vine, native to Central and South America (Day et al., 2016). This plant species is considered one of the top 10 worst weeds in the world and now is widely present in the Pacific Islands, tropical Asia, the Indian Ocean Islands, and Florida, USA (Zhang et al., 2004; Manrique et al., 2011; Day et al., 2012, 2016). *Mikania micrantha* can invade a wide range of habitats, such as various agroecosystems, natural ecosystems, disturbed areas, riverbanks, and roadsides (Zhang et al., 2004; Willis et al., 2008; Shen et al., 2013; Day et al., 2016). Due to its high rates of sexual reproduction, adaptability, capacity for compensation, and rapid growth (Lian et al., 2006; Wang et al., 2008; Shen et al., 2012, 2021), *M. micrantha* has caused significant negative ecological and economic impacts on forest vegetation, plantations, and crops in invaded habitats, resulting in significant economic losses, reductions in native species diversity, and disruptions to ecosystem services (Ismail and Mah, 1993; Willis et al., 2008; Day et al., 2012; Shrestha and Dangol, 2014; Shen et al., 2015a; Chen et al., 2024).

As a result of its high reproductive potential and its ability to grow from stem fragments, management efforts against *M. micrantha* may fail or may be largely ineffective if efforts are not properly planned and/or implemented (Zhang et al., 2004; Day et al., 2016; Clements et al., 2019). Various methods such as manual and mechanical control, chemical and cultural control practices, as well as classical biological control have been widely used (Shen et al., 2007; Ellison et al., 2008; Shen et al., 2015b, 2020; Clements et al., 2019; Day and Riding, 2019). The reliance on chemical measures is not sustainable due to its high cost, need to repeat applications, and potential harm to the environment and human health. Manual or mechanical control is labour intensive and new infestations may arise if all fragments are not destroyed (Day et al.,

2016; Clements et al., 2019).

Compared with mechanical or chemical control methods, cultural control using *Cuscuta campestris* Yuncker (Shen et al., 2007) and sweet potato (*Ipomoea batatas* [L.] Lam.) (Shen et al., 2015b, 2021) is considered more secure, ecological and sustainable for *M. micrantha* management. However, the low safety of *C. campestris* on other plants, inherently limits its potential (Costea and Tardif, 2006). Similarly, excessive cultivation of sweet potato may pose a burden on soil and agricultural systems (Onunka et al., 2011).

In contrast, biological control is one of the most effective approaches to help manage many invasive species (Winston et al., 2014). Biological control is considered environmentally-friendly due to the use of host specific organisms and is sustainable as agents remain in the field in equilibrium with the target weed (McFadyen, 1998). The rust fungus *Puccinia spegazzinii* de Toni (Pucciniaceae), which shares the same native range as *M. micrantha*, is a highly specific and effective biological control agent that targets *M. micrantha*. *Puccinia spegazzinii* can significantly slow plant growth, reduce reproductive capacity, and ultimately cause plant mortality of *M. micrantha*, through the infection of leaves, petioles, and stems (Barreto and Evans, 1995; Day et al., 2013; Day and Riding, 2019). Therefore, *P. spegazzinii* has been intentionally released into nine countries or regions: India, China, Taiwan, Papua New Guinea (PNG), Fiji, Vanuatu, Guam, Palau, and the Cook Islands, establishing in five of these, where it has contributed to the significant reduction of *M. micrantha* populations in some areas. Moreover, there have been no negative impacts on other plant species (Day et al., 2013; Winston et al., 2014; Day and Bule, 2016). It has successfully established in Taiwan of China but has not established on mainland China, despite being introduced in 2006 and 2013 (Day et al., 2013; Shen et al., 2018).

In order to effectively combat the invasion of *M. micrantha* in mainland China, we plan to re-introduce *P. spegazzinii*. However, the locations of suitable areas for *P. spegazzinii* in China remain unclear. Therefore, it is crucial to predict and assess the potential suitable areas for *P. spegazzinii* and *M. micrantha* to determine whether there are sufficient shared suitable areas for the field release of *P. spegazzinii* to suppress *M. micrantha* under current and future climate scenarios.

Ecological Niche Models (ENMs) quantify the correlation between species occurrence records and various environmental variables, thereby describing the ecological niche or habitat suitability of a species (Zimmermann et al., 2010). Commonly used ecological niche models include Genetic Algorithm for Rule Set Production (GARP) (Haase et al., 2021), BIOCLIM (Booth et al., 2014), Random Forest (RF) (Belgiu and Drăguț, 2016), and Maximum Entropy (MaxEnt) (Merow et al., 2013). Among these, the MaxEnt model is most widely applied by researchers due to its intuitive modeling approach, high predictive accuracy, ease of use, and strong interpretability (Phillips et al., 2006; Phillips and Dudík, 2008). It has been extensively used in various fields, including the prediction of potential distributions of invasive species (Padalia et al., 2014; Wan et al., 2017; Shen et al., 2024) and fungi (Yuan et al., 2015) under climate change scenarios (Thapa et al., 2018; Shabani et al., 2020; Alkhalifah et al., 2023), as well as the most appropriate regions in which to release biological control agents to control their target weeds in their introduced range. For instance, Trethowan et al. (2011) used MaxEnt to

predict what areas in South Africa are the most suitable to field release two new biological control agents against pom-pom weed, *Campuloclinium macrocephalum* (Less.) DC. (Asteraceae), while Minghetti et al. (2024) used MaxEnt to evaluate climatic suitability of regions in Australia of *Engytatus passionarius* Minghetti, Maestro and Dellapé (Heteroptera: Miridae) and its target weed stinking passionflower, *Passiflora foetida* L. (Passifloraceae) and the degree of overlap of the two species.

In this study, drawing on distribution records of *M. micrantha* and *P. spegazzinii* collected during fieldwork in various countries, along with global network data, MaxEnt models were used to predict the potential distribution of the two species in China under current and future climate scenarios. We then assessed the most promising range and its response to climate change for the field release of *P. spegazzinii*, aiming to develop more effective biological control measures to mitigate the impact of *M. micrantha* in China.

2. Materials and methods

2.1. Data collection and processing

We used the Global Positioning System (GPS) during fieldwork to collect 386 distribution records of *M. micrantha* in southwest China and 531 records of *P. spegazzinii* in Papua New Guinea, Vanuatu and Fiji, where the rust had been deliberately released and later spread. In addition, we searched the Global Biodiversity Information Facility (<http://www.gbif.org/>), other databases and the literature for additional records, particularly in other countries. From the original 6795 records for *M. micrantha* (GBIF.org (02 August (2024a))) and 98 records for *P. spegazzinii* (GBIF.org (02 August (2024b))) we downloaded from the GBIF website using basic filtering criteria, we then removed duplicate and erroneous coordinates, verified the presence of corresponding environmental variable data at occurrence locations, and applied empirical criteria to exclude biogeographically implausible records, to obtain 3,705 records of *M. micrantha* (2,446 within China, with the majority being in Taiwan) and 34 records of *P. spegazzinii* from around the world. To these records, we added a further 123 records for *M. micrantha* (All in Hainan, China) and 36 records for *P. spegazzinii* (All in Taiwan, China) from the Chinese Virtual Herbarium (<https://www.cvh.ac.cn/>), and previously published research papers. Based on these combined data, a global geographical distribution map of *M. micrantha* and *P. spegazzinii* was created (Fig. 1).

To reduce spatial sampling bias and mitigate pseudo-replication, we applied the remove duplicate occurrences function in ENMTools (Warren et al., 2010) by retaining a single representative point per

2.5'×2.5' grid cell. This resulted in 2,033 *M. micrantha* points and 313 *P. spegazzinii* points being selected for MaxEnt modeling.

2.2. Acquisition and selection of environmental variables

The environmental variables data were downloaded from WorldClim (<https://worldclim.org/>), including one topographic factor (elevation) and 19 climate factors for three periods: the current period (1970–2000), and the future periods of the 2050 s (2041–2060) and the 2070 s (2061–2080). The climate data for future periods were selected from the Beijing Climate Center Climate System Model (BCC-CSM2-MR), a model participating in the sixth phase of the Coupled Model Inter-comparison Project (CMIP6). This model has demonstrated strong performance in capturing regional climate variability and extremes (Wu et al., 2019), and it has been widely applied in species distribution studies to project current and future climate scenarios for both global and Chinese regions (Ji et al., 2024). Three Shared Socio-economic Pathways (SSPs) scenarios were chosen: SSP126, SSP245 and SSP585, representing low, medium, and high concentration emission scenarios of greenhouse gases. The spatial resolution of all environmental variables was set at 2.5 arc-minutes, a scale recognized for its precision and computational efficiency in continental-scale species distribution modeling studies (Zhao et al., 2024).

To mitigate multicollinearity effects that risk overfitting and compromised predictive accuracy (Stuhldreher and Fartmann, 2018), we conducted Pearson correlation analysis on 20 environmental variables using SPSS 27 (Supplementary Fig. 1). Predictor selection followed three steps: (1) ranking predictors by contribution rates via MaxEnt with default settings; (2) flagging strongly correlated pairs ($|r| > 0.7$); and (3) iteratively eliminating the lower-impact variable from each pair. This yielded eight variables for *M. micrantha* and four for *P. spegazzinii* in the final predictive models (Table 1).

2.3. Optimization of model parameters and model building

The MaxEnt model is sensitive to sampling biases and prone to overfitting, and modeling with the default parameters can lead to unreliable predictions (Merow et al., 2013). The predictive performance of the MaxEnt model is primarily influenced by two parameters: Feature Combination (FC) and Regularization Multiplier (RM) (Elith et al., 2011; Radosavljevic and Anderson, 2014). In this study, we optimized the parameters using the kuenm package (Cobos et al., 2019) in R v3.6.3. The process involves creating candidate models based on various FC and RM combinations, and selecting the optimal model based on statistical significance and an omission rate threshold of 5% (Cobos et al., 2019).

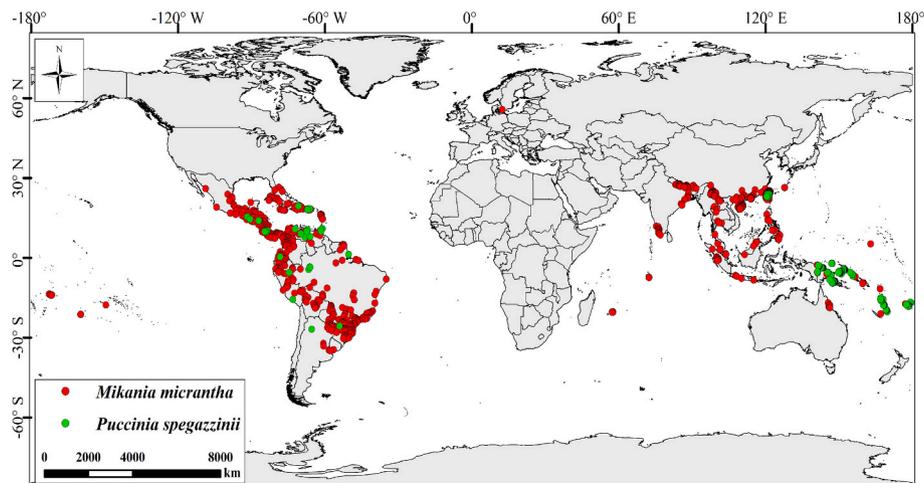


Fig. 1. Distribution of known sites of *Mikania micrantha* and *Puccinia spegazzinii* in the world.

Table 1

Environmental variables used in the model prediction for *Mikania micrantha* and *Puccinia spegazzinii*.

<i>Mikania micrantha</i>			<i>Puccinia spegazzinii</i>		
Field	Description	Unit	Field	Description	Unit
Bio2	Mean diurnal temperature range	°C	Bio2	Mean diurnal temperature range	°C
Bio7	Temperature annual range	°C	Bio7	Temperature annual range	°C
Bio8	Mean temperature of wettest quarter	°C	Bio12	Annual precipitation	Mm
Bio11	Mean temperature of coldest quarter	°C	Bio18	Precipitation of warmest quarter	Mm
Bio12	Annual precipitation	mm	–	–	–
Bio17	Precipitation of driest quarter	mm	–	–	–
Bio18	Precipitation of warmest quarter	mm	–	–	–
Bio19	Precipitation of coldest quarter	mm	–	–	–

For each species, 232 candidate models were created with 29 FCs (L, Q, P, T, H, LQ, LP, LT, LH, QP, QT, QH, PT, PH, TH, LQP, LQT, LQH, LPT, LPH, QPT, QPH, QTH, PTH, LQPT, LQPH, LQTH, LPTH, LQPTH) derived from five feature types (L = Linear, Q = Quadratic, P = Product, T = Threshold, and H = Hinge Feature) and eight RM values (0.5–4 with an interval of 0.5). Model selection was based on the Akaike minimum information criterion (AICc) values, where the optimal parameter combination corresponded to the model with the lowest AICc (Delta AICc = 0) (Cobos et al., 2019; Li et al., 2024; Miao et al., 2024; Shen et al., 2024).

2.4. Model operation and accuracy evaluation

To improve simulation accuracy, 75 % of the distribution points were randomly selected as the training data set for modeling, while the remaining 25 % were used as the test data set to validate the model. The calculations were repeated 10 times, with the repetition category set as a subsample, and the results were averaged. The maximum number of iterations for the model was set to 500, and the maximum number of background points was 10,000. The maximum number of iterations for the model was set to 500, and the maximum number of background points was 10,000. The background extent was defined by the global spatial coverage of all environmental variable layers used in this study, following the default MaxEnt protocol that randomly samples background points from the full extent of the provided environmental data (Phillips et al., 2006). As our study aims to model the species' fundamental niche across its global potential distribution, we did not apply any additional spatial constraints (e.g., species' native range polygons or biogeographic realms).

The jackknife test was used to evaluate the contributions of environmental variables and identify the dominant factors affecting the distribution of *M. micrantha* and *P. spegazzinii*. We used the area under the curve (AUC) value of the receiver operating characteristic (ROC) to test the sensitivity and specificity of the model (Bowers and Zhou, 2019; Gebrewahid et al., 2020). When the AUC value is between 0.8 and 0.9, the model performs well. If the AUC value exceeds 0.9, the model is nearly perfect (Sun et al., 2020; Luu et al., 2021). In addition, the true skill statistics (TSS) was introduced as a supplementary metric, which is significantly correlated with the AUC statistic (Allouche et al., 2006). We selected maxTSS (maximum sum of sensitivity and specificity) as the threshold and calculated the average TSS of the 10 repeated results of the MaxEnt model (Liu et al., 2016). For the TSS value, between 0.6 and 0.8 is considered useful, and values above 0.8 are excellent (Gama et al., 2017).

2.5. Classification of suitable areas

The ASCII data generated by the MaxEnt model were imported into ArcGIS v10.4 and converted to raster data. In order to maintain consistency with previous research on potential distribution of *M. micrantha* in China (Zhang et al., 2011), the global potential distribution of *M. micrantha* and *P. spegazzinii* were classified by the Jenks natural breaks method (Brewer and Pickle, 2002) as follows: for *M. micrantha*, unsuitable ($0 \leq P \leq 0.08$), slightly suitable ($0.08 < P \leq 0.24$), moderately suitable ($0.24 < P \leq 0.40$), and highly suitable ($0.40 < P \leq 1$); and for *P. spegazzinii*, unsuitable ($0 \leq P \leq 0.06$), slightly suitable ($0.06 < P \leq 0.22$), moderately suitable ($0.22 < P \leq 0.41$), and highly suitable ($0.42 < P \leq 1$). The Jenks natural break method was chosen for this study primarily because it is a widely used technique for partitioning data into distinct classes, especially for spatial data. It optimizes the natural grouping of data points and provides a clear visualization of the model's output, making it easier to interpret spatial patterns of species distribution. This method is commonly applied in species distribution modeling studies, as it effectively reflects the natural clusters within the data (Zhang et al., 2011; Shen et al., 2024; Wang et al., 2024). Subsequently, their potential distribution in China was extracted for further analysis.

2.6. Changes in distribution and overlapping suitable areas

The MaxEnt-derived suitability raster data for *M. micrantha* and *P. spegazzinii* were classified into binary outputs (suitable vs. unsuitable areas) with thresholds of 0.08 and 0.06, respectively. Using the Python-based SDMtoolboxGIS package (Brown et al., 2017) in ArcGIS, the geographic distribution changes and the overlapping suitable areas for the two species under current and future climate scenarios were calculated and analyzed.

2.7. Multivariate environment similarity surface (MESS) analysis

The MESS was employed to quantify climatic anomalies across temporal scales. It calculates similarity (S) values by comparing localized climatic parameters with baseline reference conditions during defined time intervals. Positive S-values ($S > 0$) indicate environmental congruence (higher values = greater consistency), while negative values ($S < 0$) reflect anomalies where parameters exceed historical thresholds (Elith et al., 2010). This operation was implemented by using the "density. tools. Novel" tool in the maxent.jar file.

3. Results

3.1. Optimal model and accuracy evaluation

When the model was set to default parameters (FC = LQPTH and RM = 1), Delta AICc was 149.69 for *M. micrantha*, and 48.26 for *P. spegazzinii*. However, with optimized parameters (FC = LQH and RM = 0.5 for *M. micrantha*; FC = LQP and RM = 2 for *P. spegazzinii*), Delta AICc was 0 for both species (Table 2). This optimization corresponded to 28 % and 41 % reductions in omission rates for *M. micrantha* and *P. spegazzinii*, respectively, demonstrating enhanced predictive fit to known occurrence data. Using the optimal parameters, the model

Table 2

Evaluation results of the MaxEnt model under different parameter settings.

Species	Setting	FC	RM	Delta AICc	Omission rate at 5 %
<i>Mikania micrantha</i>	Default	LQPTH	1	149.69	0.069
	Optimized	LQH	0.5	0	0.050
<i>Puccinia spegazzinii</i>	Default	LQPTH	1	48.26	0.064
	Optimized	LQP	2	0	0.038

achieved average AUC values of 0.921 ± 0.002 for *M. micrantha* and 0.978 ± 0.002 for *P. spegazzinii* (Supplementary Fig. 2), along with average TSS values of 0.886 ± 0.005 for *M. micrantha* and 0.902 ± 0.022 for *P. spegazzinii* (Table 3), indicating that the prediction results are accurate and reliable.

3.2. Major environmental variables influencing the distribution of *Mikania micrantha* and *Puccinia spegazzinii*

The jackknife test (Supplementary Fig. 3) and variable contribution analysis (Table 4) identified annual precipitation (Bio12; 65.5 %) and precipitation of warmest quarter (Bio18; 21.3 %) as the major factors governing the potential distribution of *M. micrantha*, collectively accounting for 86.8 % of explanatory power. For *P. spegazzinii*, temperature annual range (Bio7; 47 %) and precipitation of warmest quarter (Bio18; 45.7 %) emerged as key determinants, jointly explaining 92.7 % of distribution constraints.

Environmental variables are considered suitable for species survival when their occurrence probability exceeds 0.5 (Huang et al., 2020). Based on univariate modeling of major environmental variables (Supplementary Fig. 4), the ranges of factors suitable for the survival of *M. micrantha* are as follows: annual precipitation between 1648 and 3847 mm, and precipitation of warmest quarter greater than 654 mm. For *P. spegazzinii*, the ranges are: temperature annual range lower than 11 °C, and precipitation of warmest quarter between 707 and 1803 mm.

3.3. The potential distribution of *Mikania micrantha* and *Puccinia spegazzinii* in China under the current climate scenario

Under the current climate scenario, the potential suitable areas for *M. micrantha* are concentrated in southern China (Fig. 2a), with a total suitable area of $111.55 \times 10^4 \text{ km}^2$, accounting for 11.6 % of China's land area. These areas cover Taiwan, Hong Kong, Hainan, Guangdong, Guangxi, Yunnan, Fujian, Jiangxi, Hunan, Guizhou, Sichuan, Chongqing, Tibet, and Zhejiang. The highly, moderately, and slightly suitable areas account for 38.4 %, 18.1 %, and 43.5 % of the total suitable area, respectively. The highly suitable area is $42.83 \times 10^4 \text{ km}^2$, predominantly distributed in Hainan, Hong Kong, most parts of Taiwan,

Table 3

Average TSS of 10 iterations of the MaxEnt model results.

Models	TSS of <i>Mikania micrantha</i>	TSS of <i>Puccinia spegazzinii</i>
Species_0	0.883	0.877
Species_1	0.892	0.892
Species_2	0.884	0.942
Species_3	0.895	0.879
Species_4	0.887	0.892
Species_5	0.883	0.886
Species_6	0.887	0.896
Species_7	0.885	0.899
Species_8	0.876	0.930
Species_9	0.888	0.923
Mean	0.886	0.902

Guangdong, and Guangxi, as well as southern Yunnan, with small portions in southeastern Tibet and Fujian.

The suitable areas for *P. spegazzinii* are similarly concentrated in southern China (Fig. 2b). However, its overall suitability and distribution area remain significantly lower compared to *M. micrantha*. The total suitable area is $28.21 \times 10^4 \text{ km}^2$, accounting for 2.9 % of China, covering Taiwan, Hong Kong, Hainan, Guangdong, Guangxi, Yunnan and Tibet. The highly, moderately, and slightly suitable areas account for 5.7 %, 9.8 %, and 84.3 % of the total suitable area, respectively. The highly suitable area is just $3.24 \times 10^4 \text{ km}^2$ and distributed in Taiwan. In mainland China, the majority of suitable areas are classified as low suitability, with scattered moderately suitable areas distributed across Hong Kong, southern Guangxi and Guangdong, southeastern Tibet and Yunnan, and the central and northeastern parts of Hainan. Additionally, extremely limited highly suitable areas are concentrated in southern Guangxi.

3.4. The potential distribution and range change of *Mikania micrantha* and *Puccinia spegazzinii* in China under different future climate scenarios

Compared to the current climate scenario, the potential suitable areas of *M. micrantha* in China gradually expand under future climate scenarios (Fig. 3 and Supplementary Fig. 5a), extending northward entirely based on current distribution range, with no contraction

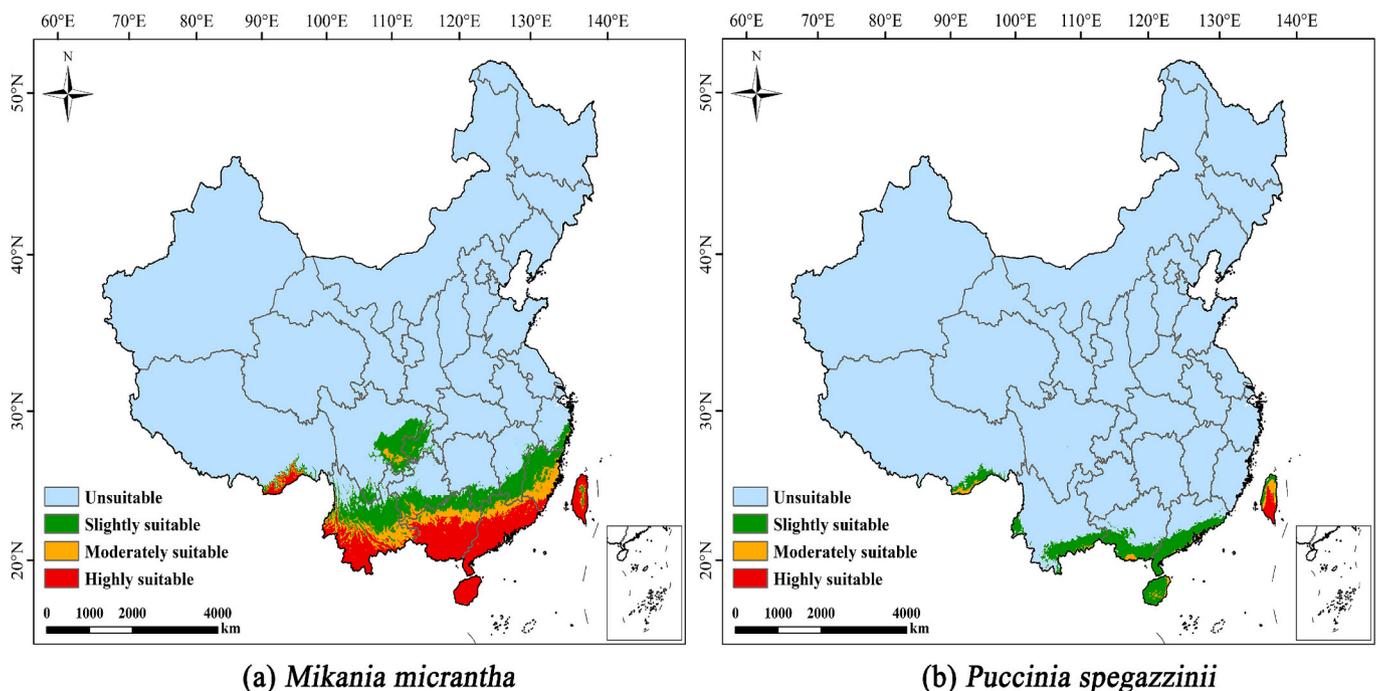


Fig. 2. Geographic distribution of potential suitable areas for *Mikania micrantha* and *Puccinia spegazzinii* in China under the current climate scenario.

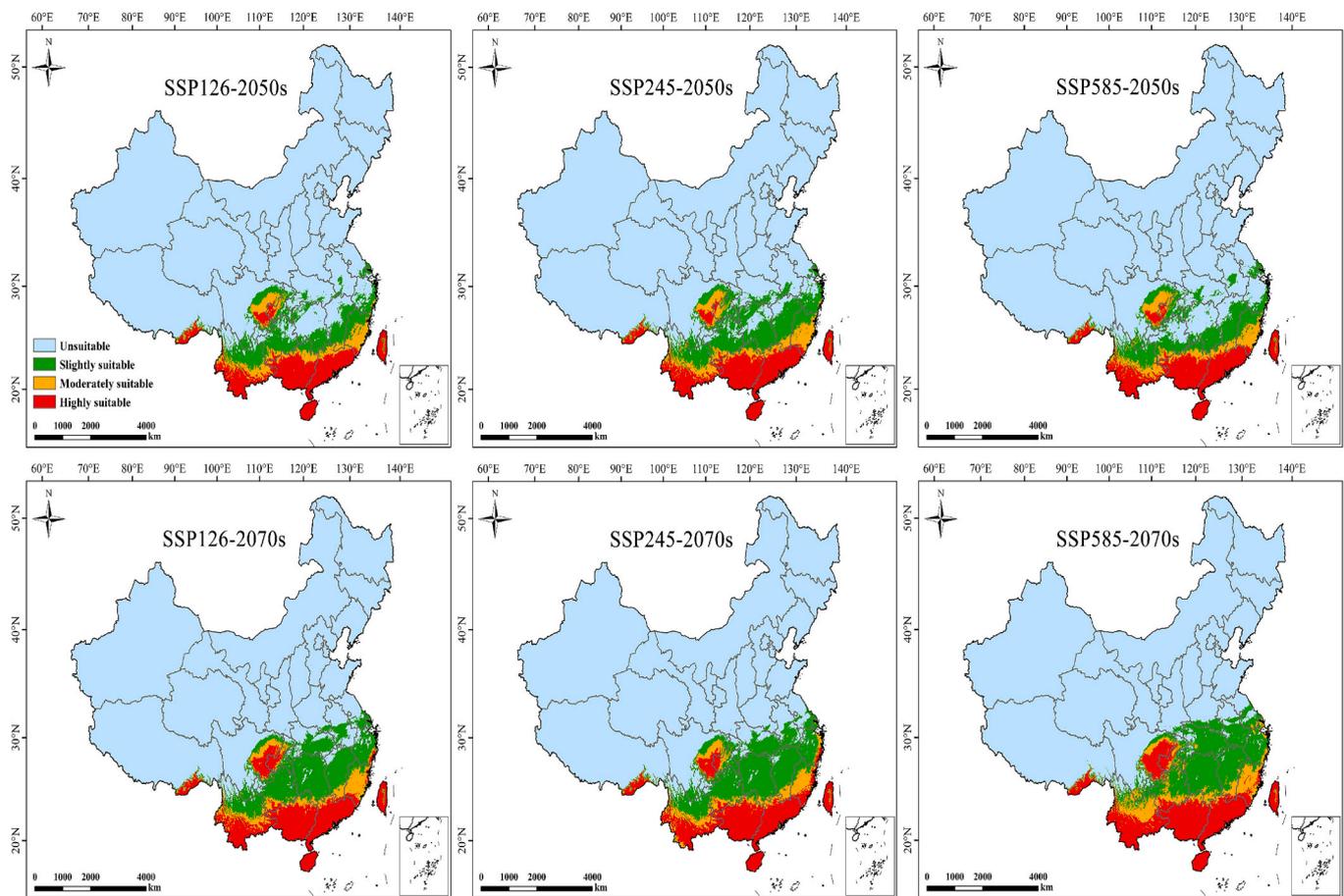


Fig. 3. Geographic distribution of potential suitable areas for *Mikania micrantha* in China under different future climate scenarios.

Table 4

Contribution rate and permutation importance of environmental variables for *Mikania micrantha* and *Puccinia spegazzinii*.

<i>Mikania micrantha</i>			<i>Puccinia spegazzinii</i>		
Environmental variable	Contribution rate (%)	Permutation importance (%)	Environmental variable	Contribution rate (%)	Permutation importance (%)
Bio12	65.5	8.8	Bio7	47	90.7
Bio18	21.3	3.2	Bio18	45.7	8.5
Bio11	9.7	62.4	Bio12	4.1	0.7
Bio17	1	1.4	Bio2	3.2	0
Bio2	0.9	2.5	-	-	-
Bio7	0.5	14.6	-	-	-
Bio19	0.5	4.2	-	-	-
Bio8	0.4	3.1	-	-	-

observed in any regions. Under SSP126, the total suitable area in the 2050 s and 2070 s is $141.97 \times 10^4 \text{ km}^2$ and $181.43 \times 10^4 \text{ km}^2$, respectively. SSP245 shows $158.48 \times 10^4 \text{ km}^2$ and $185.11 \times 10^4 \text{ km}^2$ for the same periods, while SSP585 shows $144.01 \times 10^4 \text{ km}^2$ and $205.97 \times 10^4 \text{ km}^2$. The most significant expansion occurs under SSP585 in the 2070 s, with the total suitable area increasing by $94.92 \times 10^4 \text{ km}^2$ (84.6 %), and the highly suitable area increasing by $33.98 \times 10^4 \text{ km}^2$ (79.3 %) (Fig. 5 and Supplementary Fig. 6a).

Under future climate change, the suitable areas of *P. spegazzinii* in China are projected to exhibit a declining trend, while the highly suitable habitats remain consistently concentrated in Taiwan (Fig. 4 and Supplementary Fig. 5b). Under SSP126, the total suitable area in the 2050 s and 2070 s is $18.49 \times 10^4 \text{ km}^2$ and $25.00 \times 10^4 \text{ km}^2$, respectively. SSP245 shows $23.92 \times 10^4 \text{ km}^2$ and $25.59 \times 10^4 \text{ km}^2$, while SSP585 indicates $21.14 \times 10^4 \text{ km}^2$ and $23.98 \times 10^4 \text{ km}^2$. Of these scenarios, the contraction is most notable in the 2050 s under SSP126, with the total suitable area decreasing by $9.62 \times 10^4 \text{ km}^2$ (34.2 %) and the slightly

suitable area declining by $9.62 \times 10^4 \text{ km}^2$ (40.8 %), primarily in mainland China (Fig. 6 and Supplementary Fig. 6b).

3.5. Analysis of MESS

Figs. 7 and 8 show that no climate anomaly areas ($S \geq 0$) were identified within the potential distribution of *M. micrantha* and *P. spegazzinii* under all future climate scenarios, indicating that the model-predicted environmental conditions did not exceed the climatic space of their historical distribution ranges, with low extrapolation risks. Under all scenarios (SSP126-2050 s, SSP126-2070 s, SSP245-2050 s, SSP445-2070 s, SSP585-2050 s, and SSP585-2070 s), the environmental similarity values for distribution points of *M. micrantha* and *P. spegazzinii* in China remained positive. The average similarity values for *M. micrantha* distribution points were 1.35, 1.02, 1.77, 1.17, 1.43, and 1.28 respectively, while those for *P. spegazzinii* were 0.34, 0.23, 0.40, 0.24, 0.22, and 0.33. The relatively low average similarity values at

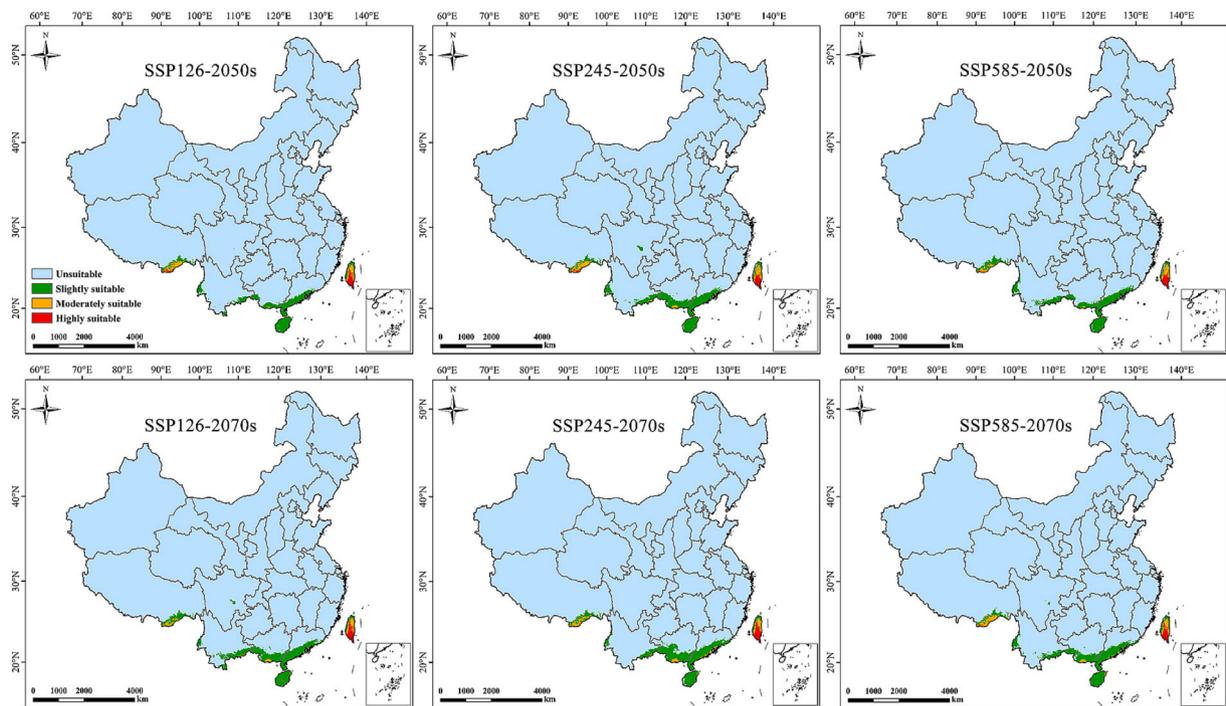


Fig. 4. Geographic distribution of potential suitable areas for *Puccinia spegazzinii* in China under different future climate scenarios.

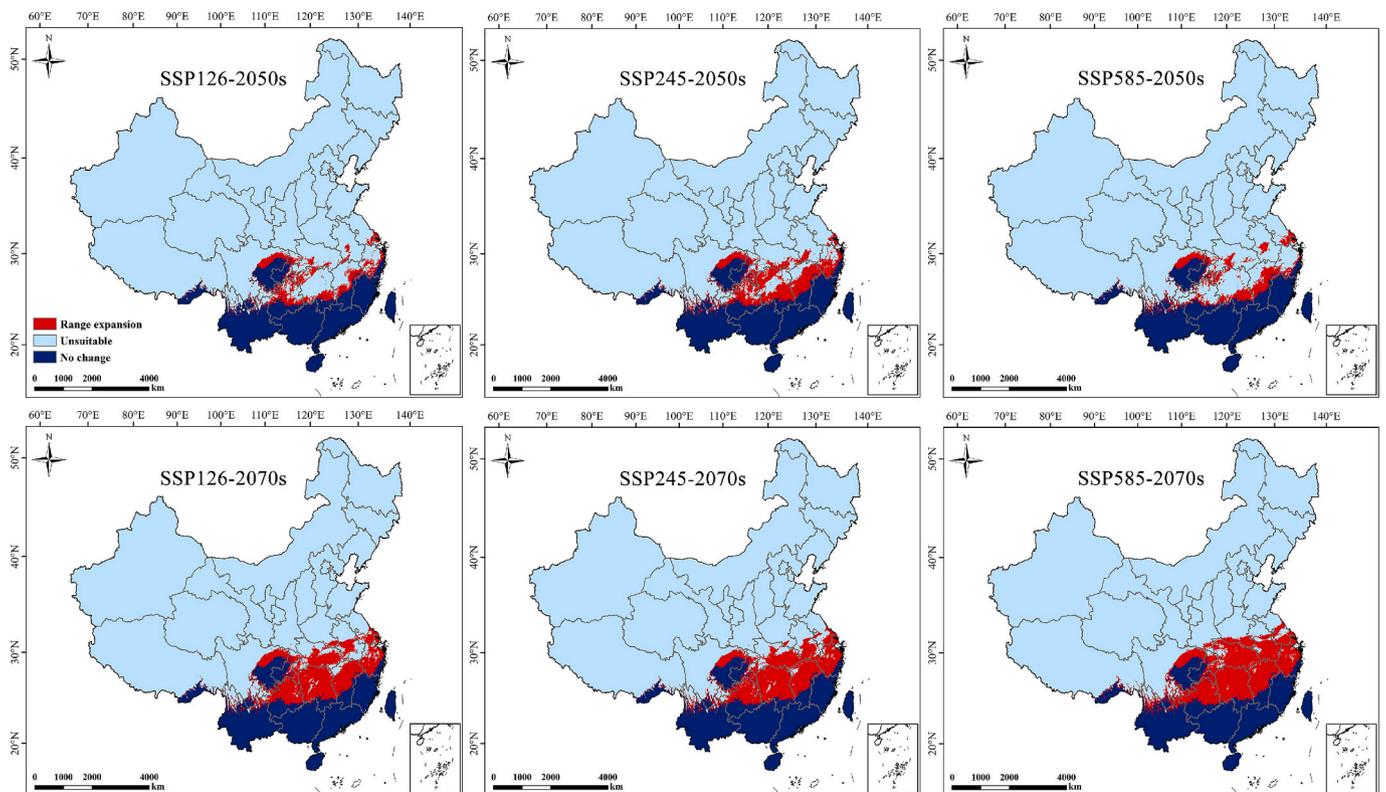


Fig. 5. Changes in the geographic distribution of potential suitable areas for *Mikania micrantha* in China under different future climate scenarios.

distribution points of both species suggest that the climatic conditions in China already lie at the edge of their historical environmental tolerance ranges, and minor future climate fluctuations may decrease the stability of suitable areas.

3.6. Overlapping suitable areas between *Mikania micrantha* and *Puccinia spegazzinii* under different climate scenarios

Under the current climate scenario (Fig. 9 and Supplementary Fig. 7), the overlapping suitable area between *M. micrantha* and *P. spegazzinii* is $28.12 \times 10^4 \text{ km}^2$, representing 25.2 % of the total

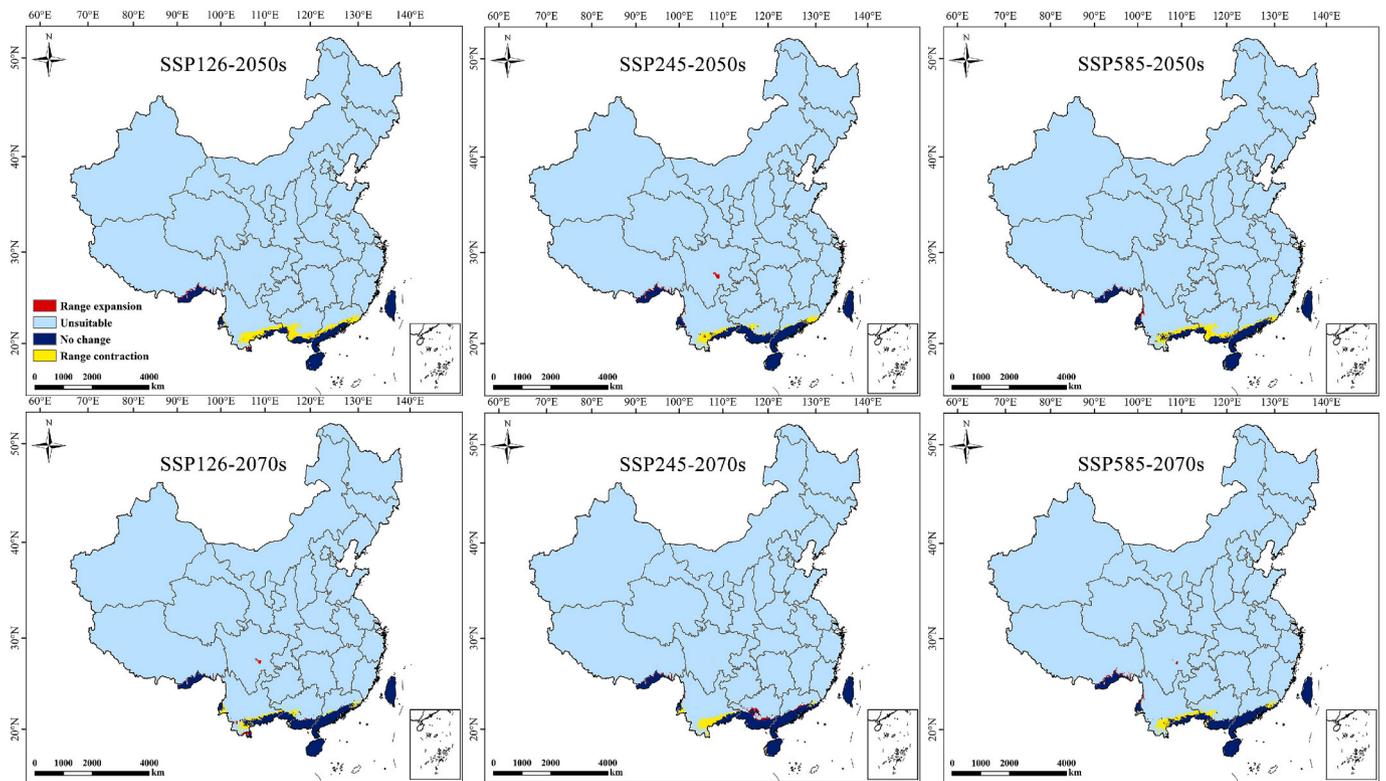


Fig. 6. Changes in the geographic distribution of potential suitable areas for *Puccinia spegazzinii* in China under different future climate scenarios.

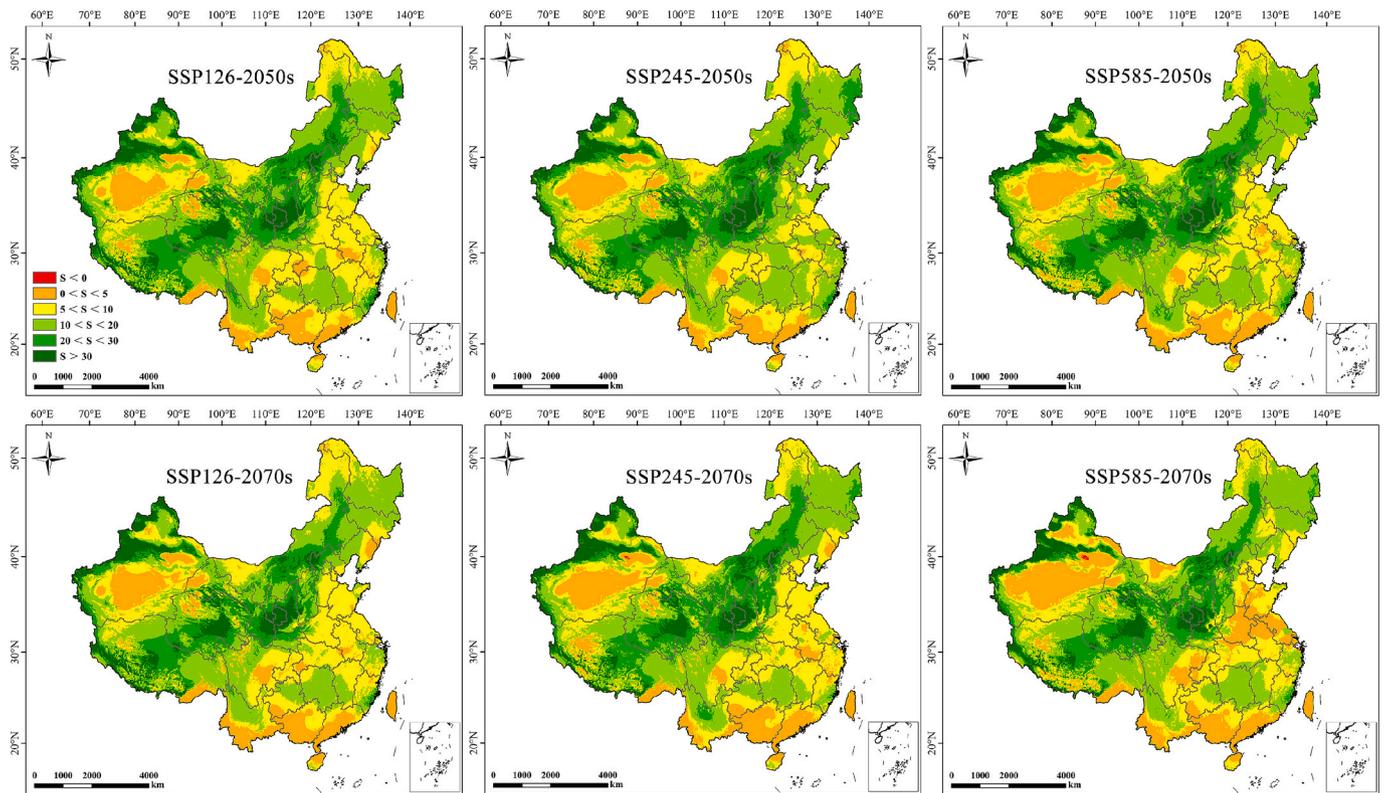


Fig. 7. Multivariate environmental similarity surface (MESS) for *Mikania micrantha* under different future climate scenarios.

potential suitable area for *M. micrantha* and 100 % for *P. spegazzinii*. It is primarily concentrated in Hainan and Taiwan, as well as the southern regions of Guangdong, Guangxi, and Yunnan, with a small portion

extending to southeastern Tibet and southwestern Yunnan. These overlapping suitable areas not only indicate regions suitable for the establishment of *P. spegazzinii*, but also highlights its potential as an

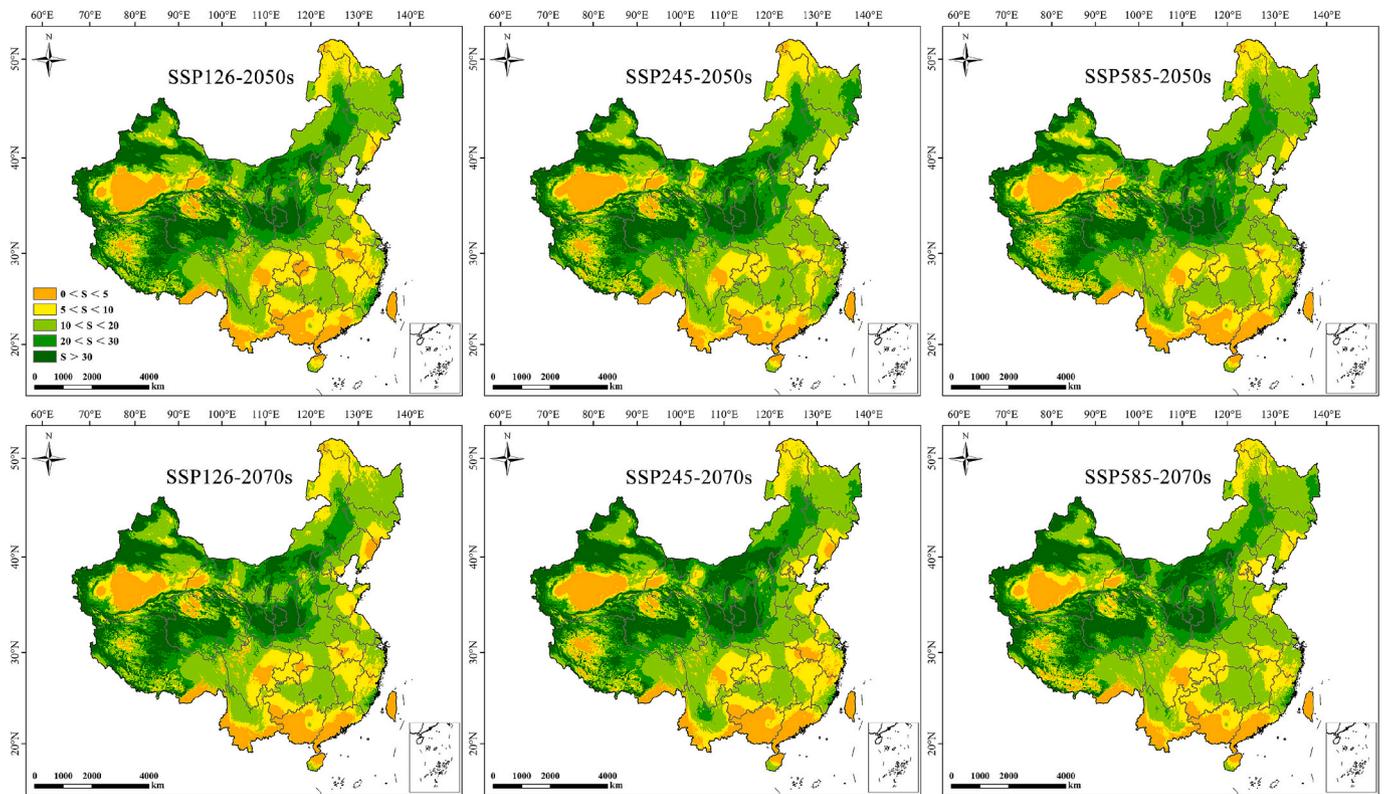


Fig. 8. Multivariate environmental similarity surface (MESS) for *Puccinia spegazzinii* under different future climate scenarios.

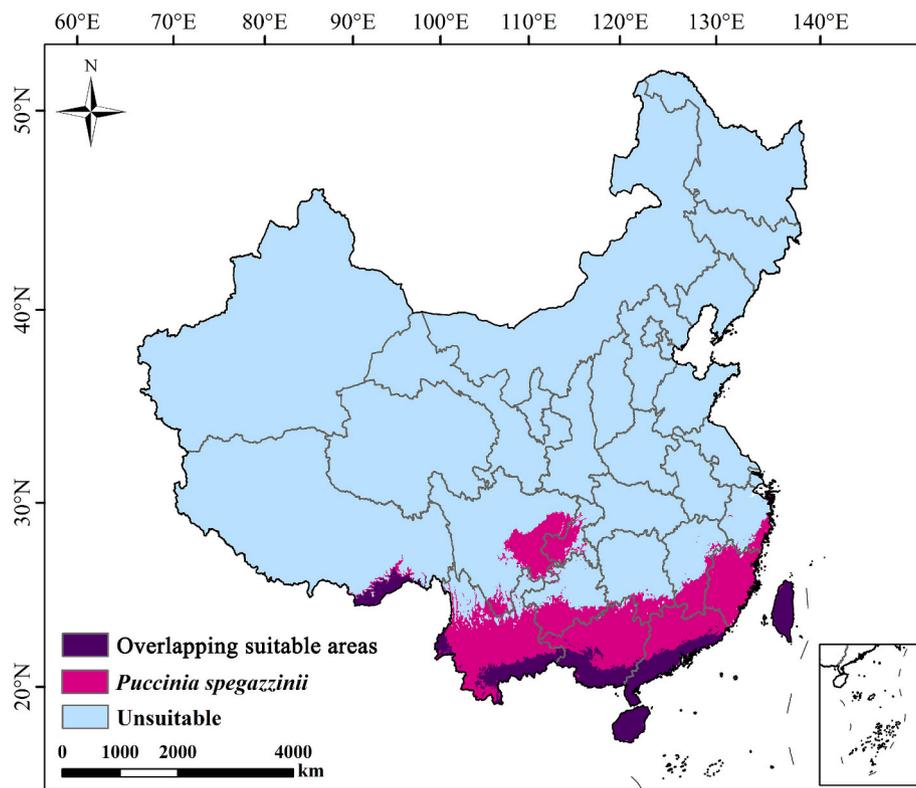


Fig. 9. Geographic distribution of overlapping suitable areas for *Mikania micrantha* and *Puccinia spegazzinii*.

effective biological control agent to curb the spread of *M. micrantha*.

Under future climate scenarios, the overlapping suitable areas between *M. micrantha* and *P. spegazzinii* show a decreasing trend compared

to the current period (Fig. 10 and Supplementary Fig. 7). Across all scenarios (SSP126-2050 s, SSP126-2070 s, SSP245-2050 s, SSP445-2070 s, SSP585-2050 s, and SSP585-2070 s), the overlapping suitable

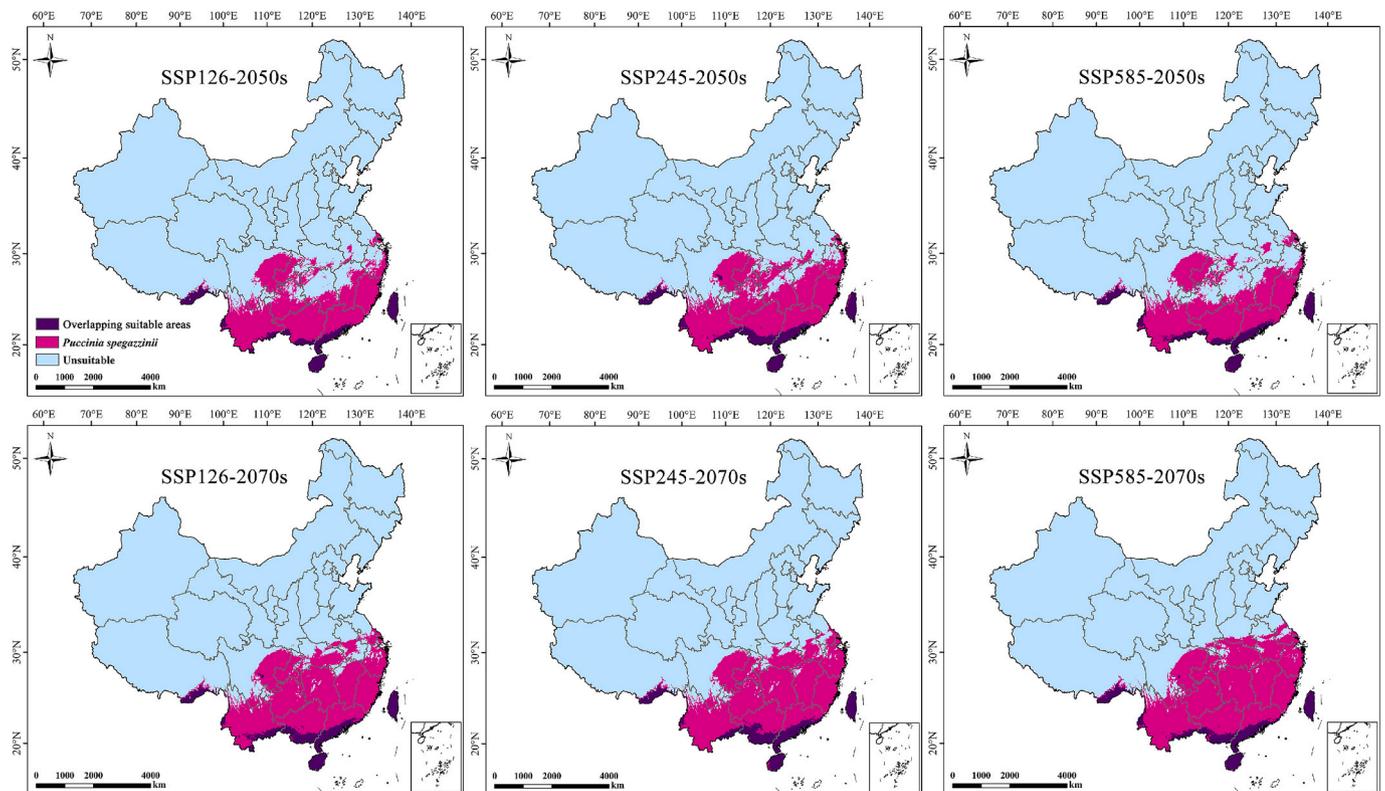


Fig. 10. Geographic distribution of overlapping suitable areas for *M. micrantha* and *P. spegazzinii* in China under different future climate scenarios.

areas are $18.49 \times 10^4 \text{ km}^2$, $25.00 \times 10^4 \text{ km}^2$, $23.92 \times 10^4 \text{ km}^2$, $25.59 \times 10^4 \text{ km}^2$, $21.14 \times 10^4 \text{ km}^2$, and $23.98 \times 10^4 \text{ km}^2$, respectively, accounting for 13.0 %, 13.8 %, 15.1 %, 13.8 %, 14.7 %, and 11.6 % of the total suitable area for *M. micrantha* during the corresponding periods. Notably, under all scenarios (including the current period), the overlapping suitable areas completely align with the suitable areas of *P. spegazzinii*, indicating that the pest control efficacy of *P. spegazzinii* inherently focuses on *M. micrantha*'s invaded regions, without requiring additional adjustments to target areas for prevention and control.

4. Discussion

The results of this study are consistent with Zhang et al. (2011) and Tu et al. (2021), who predicted that the highly suitable areas of *M. micrantha* in China would primarily be located in southern regions, including Taiwan, Hainan, Hong Kong, southern Guangxi, and southern Guangdong. On the other hand, the highly suitable areas for *P. spegazzinii* under current climate scenario are primarily concentrated in Taiwan, which aligns with previous reports on the successful establishment and spread of *P. spegazzinii* in Taiwan (Day et al., 2013; Shen et al., 2018). In contrast, the climatic suitability for *P. spegazzinii* in mainland China remains consistently low, which potentially explains why previous attempts to introduce *P. spegazzinii* as a biological agent for *M. micrantha* were unsuccessful (Winston et al., 2014). Notably, considerable climatically suitable areas persist in southern China, particularly in Guangdong Province where earlier releases were implemented. It is thought that only a limited number of releases were made in 2006 and 2011. As *P. spegazzinii* requires particular conditions such as adequate dew point and temperatures below 25 °C (Ellison et al., 2008), conditions soon after release may not have been conducive for populations of the rust to be sustained (Winston et al., 2014).

With global climate warming, the majority of plants and animals are expected to migrate toward higher latitudes and altitudes (Fang et al., 2018). The areas of suitability for *M. micrantha* will expand with the

predicted changes in climate, suggesting that it may adapt well to changing climate conditions. Unfortunately, suitable areas of *P. spegazzinii* will decrease, which makes successful introduction of *P. spegazzinii* all the more urgent. Based on the analysis of environmental variables, precipitation (Bio12 and Bio18) has been identified as the major factor influencing the potential distribution of *M. micrantha*, whereas *P. spegazzinii* is jointly influenced by both temperature and precipitation (Bio7 and Bio18). This finding explains why *P. spegazzinii* has been successfully introduced and established in several countries and regions to suppress *M. micrantha*, as they exhibit similar requirements (Ellison et al., 2008). The rust fungus infects the leaves, stems, and flowers of *M. micrantha*, restricting its growth and reproduction, thereby playing a significant role in the biological control of *M. micrantha* (Barreto and Evans, 1995; Day et al., 2013; Kumar et al., 2018; Day and Riding, 2019). In this regard, *M. micrantha* indirectly promotes the survival and spread of *P. spegazzinii* by providing a suitable host, while *P. spegazzinii* helps maintain ecosystem health and balance by suppressing the overgrowth and spread of *M. micrantha*.

Under the current climate scenario, the overlapping suitable areas between the two species account for 25.2 % of the total suitable area for *M. micrantha* and 100 % for *P. spegazzinii*, meaning that a considerable portion of the potential distribution range of *M. micrantha* is suitable for the field release of *P. spegazzinii*. Although the overlapping suitable areas between the two species are projected to decrease under future climate scenarios, their proportion relative to *M. micrantha*'s total suitable areas remains relatively stable (11.6 % – 15.1 %) and consistently aligns with the suitable areas of *P. spegazzinii*, indicating that climate change is unlikely to significantly weaken their spatial coupling relationship. However, it is important to note that while considerable areas of southern China are potentially suitable for the rust, achieving establishment still requires learning from efforts in other countries where *P. spegazzinii* has established, and past unsuccessful efforts in mainland China. Adopting an even more conservative approach such as releasing the rust initially in only highly favourable microclimatic areas, i.e. moist

shady areas, with cool night time temperatures and in the most appropriate season, where conditions for sporulation are conducive, as well as ensuring appropriate release techniques are employed over space and time should increase the chance of establishment and hopefully, with time, control of *M. micrantha*.

This study elucidates the distribution dynamics of *M. micrantha* and *P. spegazzinii* under current and future climate scenarios in China. Consistent with the findings of Trethowan et al. (2011) on *C. macrocephalum*, integrating native and invasive data with parameter optimization significantly enhanced model accuracy. However, unlike the 96 % niche overlap observed between *E. passionarius* and its host *P. foetida* in Minghetti et al. (2024), while *P. spegazzinii*'s current suitable areas are fully encompassed by *M. micrantha*, its projected range contraction under future climate scenarios may undermine the biocontrol potential of the rust fungus. This discrepancy highlights the species-specific climatic responses of biological control agents: the rust fungus is constrained by both precipitation and temperature, whereas *M. micrantha* depends primarily on precipitation. Therefore, priority should be given to releasing strains of the rust fungus in moderate-to-high suitability areas within mainland China, particularly the highly suitable areas exclusively concentrated in Fangchenggang City, southern Guangxi Province under current condition (Fig. 2b), while monitoring their adaptive evolution. Additionally, similar to the data bias issues noted in Trethowan et al. (2011), future studies should incorporate experimental data on the rust fungus in high-latitude regions to validate model predictions of northward range expansion.

5. Conclusion

Predicting the potential distribution of invasive plants and their biological control agents under climate change is crucial for invasive species management and biodiversity conservation. Our study demonstrates that the distribution of the invasive plant *M. micrantha* is predominantly driven by precipitation, whereas its biological control agent, *P. spegazzinii*, exhibits climatic dependencies jointly determined by both temperature and precipitation. The suitable areas for the two species are concentrated in southern China, with *M. micrantha* exhibiting broader adaptability compared to *P. spegazzinii*. Under future climate scenarios, the suitable areas for *M. micrantha* in China are projected to expand northward, while *P. spegazzinii* exhibit a contracting trend. Furthermore, although the overlapping suitable areas between *M. micrantha* and *P. spegazzinii* show a reduction compared to current scenario, they remain relatively stable and perfectly align with the suitable areas of *P. spegazzinii*, indicating its promising potential as a targeted biocontrol agent against *M. micrantha*. Key regions such as Hong Kong, Hainan, Guangdong, Guangxi, Tibet and Yunnan represent the primary overlapping suitable areas for the two species in mainland China. Therefore, field releases and the establishment of *P. spegazzinii* in these regions should be seriously considered to enhance the control and management of *M. micrantha*. This work provides guidance for the implementation of invasive plant control measures, offers insights for the rational introduction and application of biological control agents, and delivers scientific evidence for improving early warning and response strategies for invasive species in the future.

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Data availability statement.

The raw data supporting the conclusions of this article will be made available by the corresponding author Shicai Shen, without reservation.

CRediT authorship contribution statement

Wei Zhang: Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Qing Huang:** Visualization, Methodology, Formal analysis, Data curation. **Yingzhi Kuang:** Visualization, Methodology, Formal analysis, Data curation. **David Roy Clements:** Writing – review & editing, Conceptualization. **Gaofeng Xu:** Methodology, Investigation, Conceptualization. **Fudou Zhang:** Project administration, Investigation, Conceptualization. **Shicai Shen:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization. **Lun Yin:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Michael Denny Day:** Writing – review & editing, Data curation, Conceptualization.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocontrol.2025.105754>.

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