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## **► To cite this version:**

Xiao Hu, Guiling Ding, Fangzhou Ma, Muhammad Naeem, Yong Li, et al.. The cuckoo bumble bee, *Bombus chinensis*, has a fragmented habitat, as revealed using the maximum entropy approach (Hymenoptera: Apidae). *Apidologie*, 2022, 53 (4), pp.36. <10.1007/s13592-022-00942-5>. <hal-04169180>

**HAL Id: hal-04169180**

**<https://hal.science/hal-04169180v1>**

Submitted on 24 Jul 2023

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# The cuckoo bumble bee, *Bombus chinensis*, has a fragmented habitat, as revealed using the maximum entropy approach (Hymenoptera: Apidae)

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Received 2 September 2021 – Revised 14 May 2022 – Accepted 25 May 2022

**Abstract** – As vital pollinators, bumble bees play an important role in ecology and agricultural economy, but the decline in diversity and abundance has received widespread attention. Bumble bees of the subgenus *Psithyrus* are obligate social parasites that invade the nests of other bumble bees as part of their life cycle. This dependency on other colonies may make *Psithyrus* bumble bees vulnerable to decline and extinction. Hence, conservation strategies and potentially suitable habitats should be identified for these vulnerable species. Here, the potential distribution of a cuckoo bumble bee endemic to China, *Bombus (Psithyrus) chinensis* (Morawitz 1890) (Hymenoptera, Apidae), was predicted based on species distribution data and ten bioclimatic or environmental variables. Four important variables, namely, the minimum temperature of the coldest month, growing degree days, isothermality, and mean temperature of the warmest quarter, contributed the most to the distribution model. The maximum entropy method (MaxEnt) revealed that the potential distribution of *B. chinensis* was fragmented under current climate conditions. The areas of potential habitat with low suitability, moderate suitability, and high suitability were 455,451 km<sup>2</sup>, 170,260 km<sup>2</sup>, and 116,111 km<sup>2</sup>, respectively. Eight provinces were evaluated as critical regions for *B. chinensis* conservation, especially Sichuan, Xizang, Yunnan, and Ningxia Provinces. In conclusion, the results reveal a cuckoo bumble bee's fragmented distribution and provide a basis for its conservation strategies. The areas identified as highly suitable for *B. chinensis* should be considered primary conservation areas.

***Bombus chinensis* / conservation / cuckoo bumble bee / distribution / social parasitism**

## 1. INTRODUCTION

As bumble bees are important pollinators and play critical roles in natural ecosystems and agricultural food production worldwide, their decline has caught the attention of global scientists in recent decades (Potts et al. 2010; Brown

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Manuscript editor: Mathieu Lihoreau

2011; Cameron et al. 2011; Goulson et al. 2015; Cameron and Sadd 2020). Among bumble bees, those of the subgenus *Psithyrus* have a unique lifestyle in that they rely on their hosts for the successful rearing of their young ones (Andersson 1984; Lhomme and Hines 2019). This reliance on the host for reproduction is similar to that of the well-known cuckoo bird that tricks its hosts to raise its offspring, which is why members of the subgenus *Psithyrus* are commonly called “cuckoo bumble bees” (Yang et al. 2017; Brasero et al. 2018). They not only drop their eggs into host nests but also use the social systems of their hosts. Hence, they are also called “social parasites” (Andersson 1984; Kilner and Langmore 2011). Furthermore, bumble bees of *Psithyrus* lack a worker caste, a pollen-collecting apparatus on the posterior tibiae, and the ability to produce wax for nest building (Dronnet et al. 2005; Bunk et al. 2010). This unique lifestyle always threatens cuckoo bumble bees because of the risk of extinction of their hosts (Suhonen et al. 2015, 2016). Therefore, the assessment of suitable areas and prediction of the potential distribution of cuckoo bumble bees under current and future scenarios are important for the development of further research and conservation strategies.

Social parasitic species are classified into two groups: facultative social parasites (e.g., *Bombus rufocinctus* Cresson or *Bombus veteranus* (Fabricius) (Virostek 1953; Hobbs 1965)) and obligate social parasites (e.g., the subgenus *Psithyrus* and *Bombus inexpectatus* (Yarrow 1970; Müller 2006)), according to their mode of parasitism (Lhomme and Hines 2019). Although the host has been recorded for only 15 of the 29 bumble bee species of *Psithyrus*, the typical representation of social parasitism has been shown by this subgenus (Williams 1998). The bumble bee *Bombus chinensis* (Morawitz 1890) (Hymenoptera, Apidae), also a member of the subgenus *Psithyrus*, known as the cuckoo bumble bee, is endemic to China and is mainly distributed from the eastern part of the Qinghai-Tibet Plateau to the southern part of Xizang (An et al. 2011). Reinig (1935) reported this species as a socially parasitic species and described its potential host

as *Bombus pyrosoma* (Reinig 1935). However, no *B. chinensis* specimens were found in the *B. pyrosoma* nests to confirm this hypothesis (Reinig 1935; Lhomme and Hines 2019). Moreover, scant information is available due to the unique lifestyle of this cuckoo bumble bee, and similarly, the available data are also scarce. Therefore, species distribution modeling could be an effective approach for predicting the distribution of *B. chinensis*, which is important for researching and conserving this bumble bee (Pearson et al. 2007; Elith and Leathwick 2009).

Multiple ecological niche approaches are available for the estimation of species distribution models (SDMs), and various studies have shown that the maximum entropy model (MaxEnt) is an effective analytical tool for SDMs (Wang et al. 2017; Thapa et al. 2018; Zhang et al. 2018). MaxEnt is a general method for making predictions or inferences from incomplete information. The idea of MaxEnt is to estimate the target probability distribution by using presence-only datasets to find the probability distribution of maximum entropy and subject it to a set of constraints, which represent incomplete information about the target distribution (Phillips et al. 2006). The available information about the target distribution is usually expressed as a set of real-valued variables, called “features” (including climate variables, elevations, soil categories, vegetation types, or other environmental variables and their effects), and constraints are the average expected values of each feature (Elith et al. 2006). When MaxEnt is applied to the presence-only distribution model, pixels in the study area constitute the space in which the MaxEnt probability distribution is defined (Araujo et al. 2005). The MaxEnt approach has also been proven to be an effective tool for predicting and evaluating the distributions of other bumble bee species (Penado et al. 2016; Naem et al. 2018, 2019; Krechmer et al. 2020). In particular, this approach also effectively assessed the potential distribution of the invasive bumble bee species *Bombus terrestris* in China, Japan, and South America (Kadoya et al. 2009; Aizen et al. 2018; Marshall et al. 2018; Naem et al. 2018).

In this study, we used open-source software with geographic reference records and bioclimatic or environmental factors to evaluate the potential habitats and the most important factors affecting the distribution of the endemic cuckoo bumble bee *B. chinensis* in China. This study aims to (1) identify the vital bioclimatic or environmental factors affecting the distribution of *B. chinensis*, (2) model the spatial range of suitable *B. chinensis* habitats using current climate scenarios, and (3) identify and evaluate the important provinces where *B. chinensis* is distributed to provide basic knowledge for the development of further research and conservation strategies.

## 2. MATERIALS AND METHODS

### 2.1. Sample data

Sample data of the bumble bee *B. chinensis* were obtained via historical collections and field sampling. Fifty-five specimen records from 1963 to 2018 were collected from the Institute of Zoology, the Chinese Academy of Sciences, and the Institute of Apicultural Research, the Chinese Academy of Agriculture Science. In 2019, we investigated the provinces where historical sampling sites were located (including Gansu, Ningxia, Shaanxi, Sichuan, Xizang, and Yunnan) and collected eight specimens of *B. chinensis*. Specimens were sampled, and their location information was acquired with a handheld GPS device (Garmin cs60). There were 63 presence records (22 records in Ningxia, 14 in Gansu, 11 in Yunnan, 10 in Sichuan, 4 in Xizang, and 2 in Shaanxi) (Figure 1). The adjacent modeled sampling sites were thinned by less than 30 km (Naeem et al. 2018; Hu et al. 2021). Data thinning was performed using the spThin R package (version 0.2.0) (Aiello-Lammens et al. 2015; Santana et al. 2019).

### 2.2. Bioclimatic or environmental data

Twenty-three bioclimatic or environmental variables were implemented here for the

development of models, where the nineteen bioclimatic variables at a 2.5-min resolution (~5 km) were downloaded from the WorldClim-Global climate dataset (<https://www.worldclim.org/data/worldclim21.html>) and four other environmental variables for the current period (1970–2000), (1) growing degree days (30 arcmin (~50 km)), (2) rainy days (5 arcmin (~10 km)), (3) global reference evapotranspiration (Global-ET0, 30 arcsec (~1 km)), and (4) radiation of the warmest quarter (bio\_26) (10 arcmin (~20 km)), which are related to the bumble bee distribution, were obtained, respectively, from the Atlas of the Biosphere, the Nelson Institute Center for Sustainability and the Global Environment, University of Wisconsin-Madison (<https://sage.nelson.wisc.edu/data-and-models/atlas-of-the-biosphere/mapping-the-biosphere/ecosystems/growing-degree-days/>), Climate Change Agriculture And Food Security (CCAFS) ([http://ccafs-climate.org/data\\_spatial\\_downscaling/](http://ccafs-climate.org/data_spatial_downscaling/)), Consultative Group for International Agriculture Research (CGIAR) (<https://cgiarcsi.community>), and Global Climatologies for Bioclimatic Modeling (Climond) (<https://www.climond.org/BioclimRegistry.aspx>) (Table I) (Williams et al. 2014; Zhang et al. 2018; Wang et al. 2019).

To avoid multicollinearity between the variables, the Pearson correlation coefficient was used to select the variables with low correlations (De Marco and Nóbrega 2018; Wang et al. 2019). The Pearson correlation coefficient  $r$  of pairwise variables was calculated with the “PerformanceAnalytics” R package (version 2.0.4, <https://github.com/braverock/PerformanceAnalytics>). Only variables with a pairwise correlation coefficient less than 0.8 were retained. If the correlation was greater than 0.8, the variable with the most significant contribution according to the contribution percentage was selected.

### 2.3. Modeling procedure and GIS analyses

MaxEnt was used to evaluate the potential distribution of *B. chinensis* following the flow chart shown in Figure 2. We fit an initial model with



**Figure 1.** Current distribution of *B. chinensis*.

the thinned sampling sites and twenty-three bioclimatic or environmental variables with MaxEnt (version 3.4.1; <http://www.cs.princeton.edu/>). In the initial model, “Random test percentage” was set to 25, and the “Do jackknife to measure variable importance” and “Make pictures of predictions” options were selected. The rest of the

settings were set to default. Then, the methods described in Sect. 2.2 were used to evaluate the relevant variables. The distribution of *B. chinensis* was simulated with the thinned sampling sites and filtered variables. The “response curves” option was chosen, and the other model settings were consistent with the initial model settings.

**Table I** Information on the 23 bioclimatic or environmental variables

Symbol	Bioclimatic/environmental variables	Units
bio_01	Annual mean temperature	°C
bio_02	Mean diurnal range (mean of monthly (max temp-min temp))	°C
<b>bio_03</b>	<b>Isothermality (bio_02/bio_07) (<math>\times 100</math>)</b>	-
bio_04	Temperature seasonality (standard deviation $\times 100$ )	-
bio_05	Max temperature of warmest month	°C
<b>bio_06</b>	<b>Min temperature of coldest month</b>	°C
bio_07	Temperature annual range (bio_05-bio_06)	°C
bio_08	Mean temperature of wettest quarter	°C
bio_09	Mean temperature of driest quarter	°C
<b>bio_10</b>	<b>Mean temperature of warmest quarter</b>	°C
bio_11	Mean temperature of coldest quarter	°C
bio_12	Annual precipitation	mm
<b>bio_13</b>	<b>Precipitation of wettest month</b>	<b>mm</b>
<b>bio_14</b>	<b>Precipitation of driest month</b>	<b>mm</b>
<b>bio_15</b>	<b>Precipitation seasonality (coefficient of variation)</b>	-
bio_16	Precipitation of wettest quarter	mm
bio_17	Precipitation of driest quarter	mm
bio_18	Precipitation of warmest quarter	mm
bio_19	Precipitation of coldest quarter	mm
<b>bio_26</b>	<b>Radiation of warmest quarter</b>	<b>W/m<sup>2</sup></b>
<b>gdd</b>	<b>Growing degree days</b>	<b>days</b>
<b>et0</b>	<b>Global reference evapo-transpiration</b>	<b>mm/days</b>
<b>rds</b>	<b>Rainy days</b>	<b>days</b>

The candidate bioclimatic or environmental variables are in bold

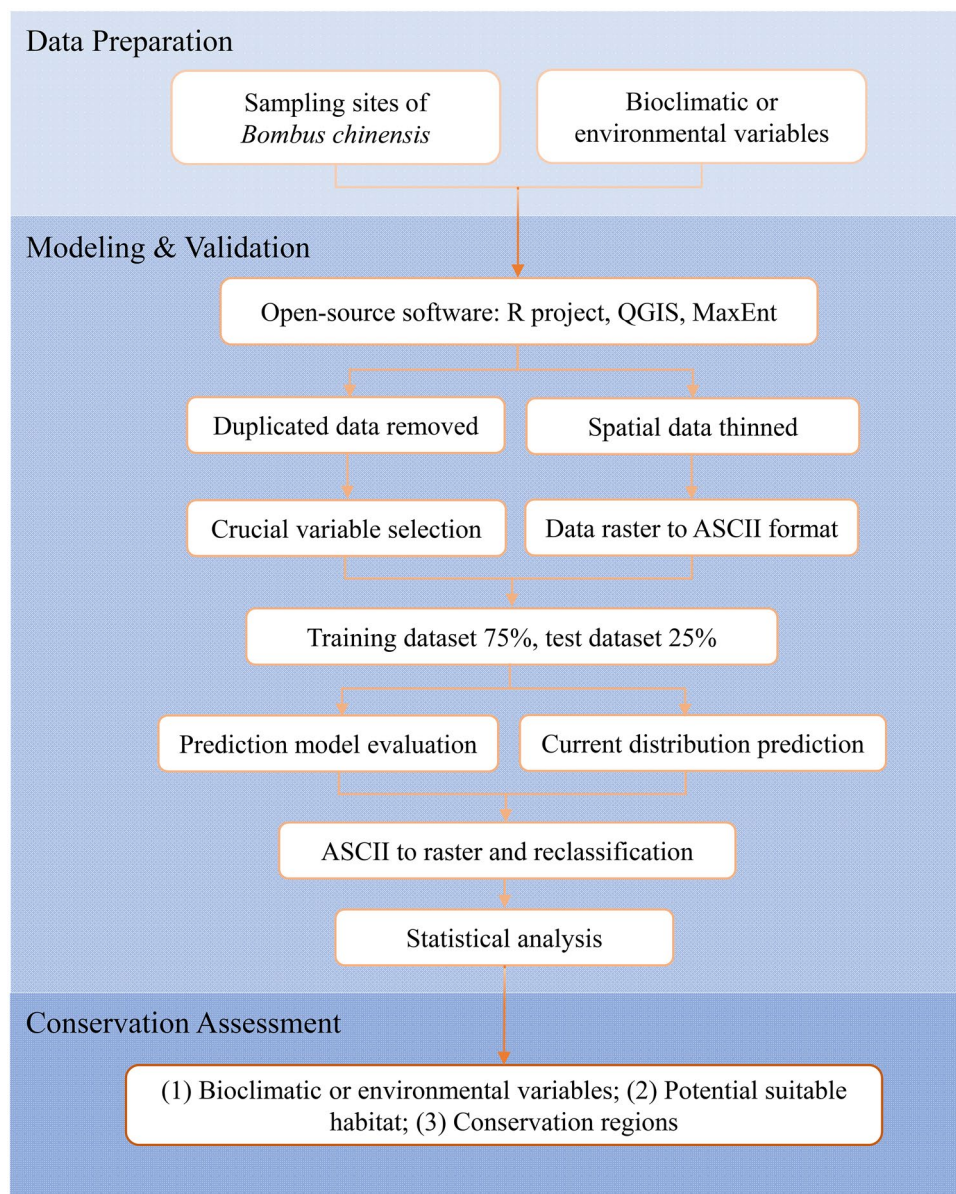
To improve the effectiveness of estimating species prevalence, we converted the species suitability threshold into binary prediction and then estimated species prevalence as the proportion of predicted presence among the background data points in the test dataset (Li and Guo 2013). We varied the number of background data in the test dataset: 100, 200, 500, 1000, 2000, 5000, and 10 000, and the test percentage was 25% and 50%.

## 2.4. Model evaluation

Variable importance was determined by the contribution of bioclimatic or environmental variables to the distribution prediction and

the jackknife procedure. The receiver operating characteristic (ROC) curve was based on model accuracy according to independent threshold evaluation (Araujo et al. 2005; Wang et al. 2019). The ROC curve was plotted using the calculated 1-specificity as the abscissa and the 1-omission rate as the ordinate, yielding area under the curve (AUC) values between 0.5 and 1.0. The evaluation criteria are simulation “failure,” 0.5–0.6; “fair,” 0.7–0.8; “good,” 0.8–0.9; and “excellent,” 0.9–1.0 (Wang et al. 2017).

Moreover, to avoid misleading indicators in AUC tests, we also used the true skill statistic, TSS and Sørensen’s similarity index and *F*-measure, to check the final model to ensure the accuracy of the distribution model



**Figure 2.** Flowchart showing the methodology used in this study.

(Jiménez-Valverde 2012, 2014; Leroy et al. 2018). Values of the *F*-measure range from 1 to 0, with 1 indicating that the prediction fully conforms to the observation without any false positives or false negatives, while 0 means that none of the predictions are consistent with any

observations. Relative to the number of true presences, the lower the similarity value is, the higher the number of false positives and false negatives (Leroy et al. 2018). When the TSS value  $\geq 0.5$ , the model is considered acceptable (Naeem et al. 2018).

## 2.5. Spatial conservation assessment

The classification of habitat suitability for *B. chinensis* was as follows: (1) AUC = 0–0.50 indicated “unsuitable”; (2) AUC = 0.50–0.75 indicated “low suitability”; (3) AUC = 0.75–0.90 indicated “moderate suitability”; and (4) AUC = 0.90–1.00 indicated “high suitability” (Naeem et al. 2019; Hu et al. 2021). In addition, the suitable areas were determined by the raster calculator (Naeem et al. 2018; Zhang et al. 2018). The vital distribution regions of *B. chinensis* were assessed to provide reasonable suggestions for conservation strategies. The area and proportion of different categories of habitat suitability were determined and assigned to the corresponding administrative divisions of China. The suitable area in each province was classified to propose conservation priorities. Moreover, we overlapped the potential suitability of *B. chinensis* with the nature reserve in China, which was downloaded in “ArcGisFeatureServer” in QGIS software. Then, the overlap area and proportion have been calculated to evaluate its conservation status.

## 3. RESULTS

### 3.1. Environmental variable selection and prediction accuracy

The 10 bioclimatic or environmental variables with low correlations and a high contribution rate were screened through Pearson correlation and contribution percentage analyses. These variables were isothermality (bio\_02/bio\_07) ( $\times 100$ ) (bio\_03), minimum temperature of the coldest month (bio\_06), mean temperature of the warmest quarter (bio\_10), precipitation of the wettest month (bio\_13), precipitation of the driest month (bio\_14), precipitation seasonality (coefficient of variation) (bio\_15), radiation of the warmest quarter (bio\_26), global reference evapotranspiration (et0), rainy days (rds), and growing degree days (gdd) (Table I and Figure 3). The Pearson correlation coefficients between all pairs of variables were less than

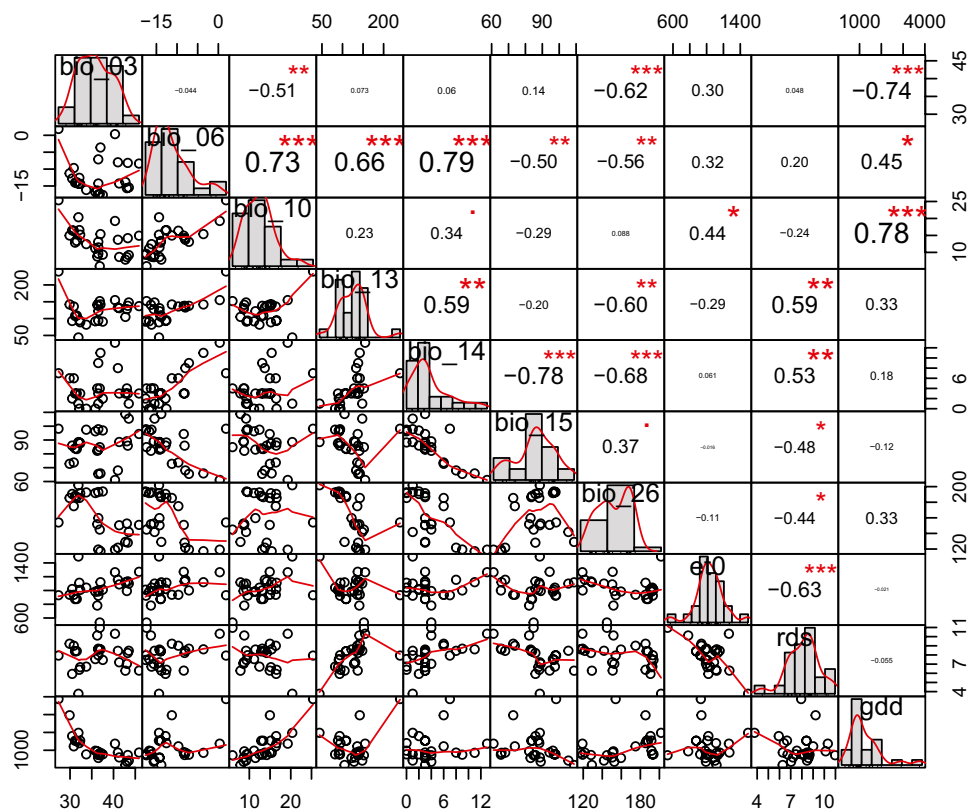
0.8, and the cumulative contribution rate of the eleven variables was 99.9%.

Through repeated debugging of model parameters and evaluation, we finally obtained the final model with a background dataset of 200 and a test percentage of 50%. AUC value of 0.938, the value of TSS was 0.620; value of *F*-measure was 0.529 and had better performance (Supplementary Table S1).

### 3.2. Bioclimatic or environmental variable contributions

In the current distribution model of *B. chinensis*, four bioclimatic or environmental variables were the most important: minimum temperature of coldest month, growing degree days, isothermality, and mean temperature of the warmest quarter. The contribution values of the minimum temperature of the coldest month and growing degree days both exceeded 0.8, which were significantly higher than the values of the other environmental variables. However, precipitation seasonality had the least influence on the modeling (Figure 4A).

Statistical analysis showed that the ranges and standard deviations of the 10 bioclimatic or environmental variables gradually decreased with increasing suitability level, indicating that the occurrence probability of *B. chinensis* gradually increased with increasing suitability level (Table II). With a decline in suitability level, indicating more stringent requirements in the environment, the distribution range decreased gradually. The environmental conditions underlying the highly suitable habitat of *B. chinensis* were as follows: an average isothermality of 46.78, an average radiation of the warmest quarter of 116.74 W/m<sup>2</sup>, and an average number of rainy days in the warmest season of 16.20 days. The optimal environmental conditions of the moderately suitable areas were as follows: a mean temperature of the warmest quarter of 7.96 °C, a minimum temperature of the coldest month higher than −14.87 °C, a mean precipitation seasonality of 40.10, a mean growing degree day of 432.24 days, and a global reference average



**Figure 3.** Bioclimatic or environmental variable correlation analysis of the distribution of *B. chinensis*. The symbols “\*\*\*”, “\*\*”, and “\*” represent significance levels of  $p$  values of “0–0.001”, “0.001–0.01”, and “0.01–0.05”, respectively.

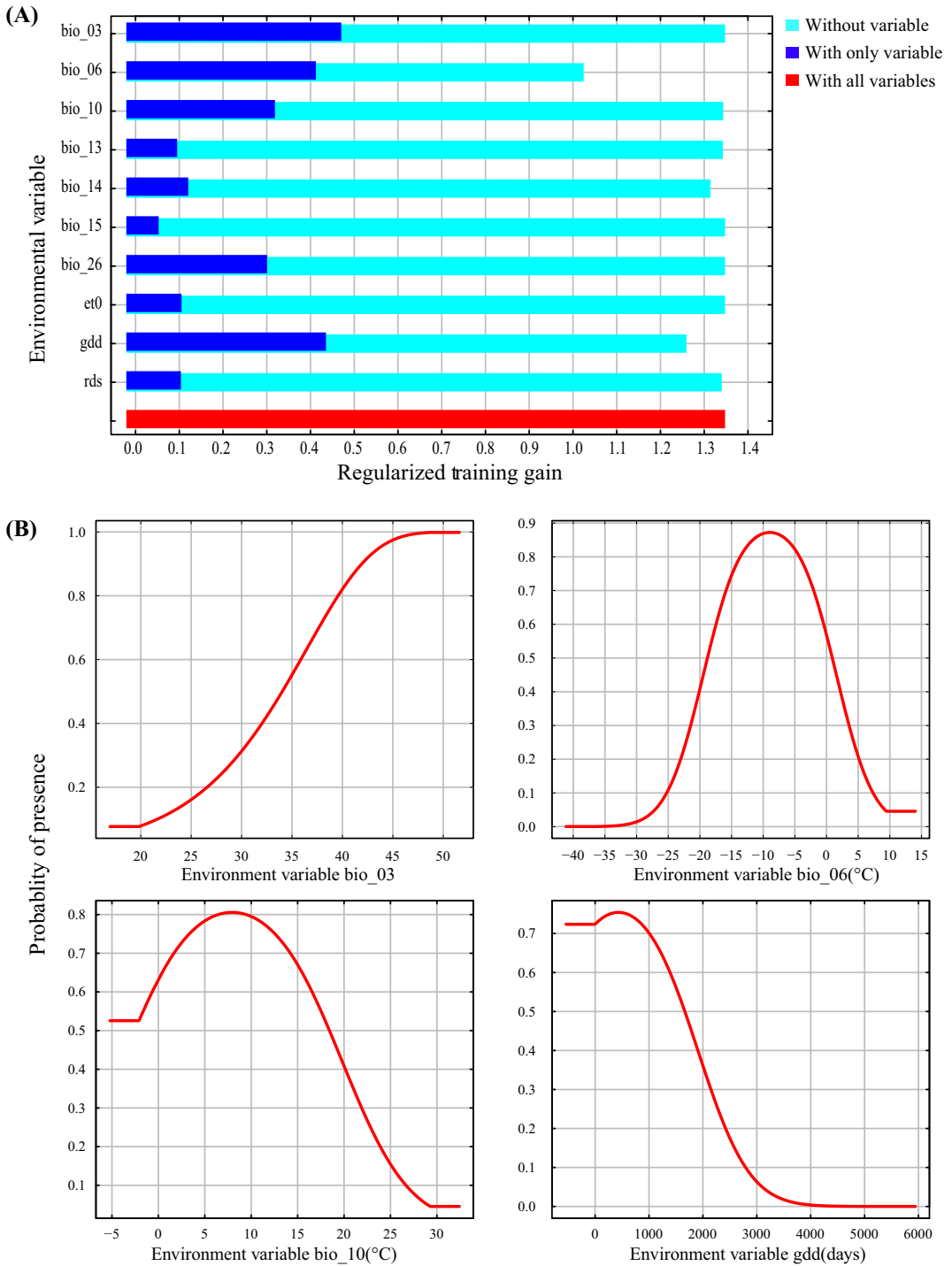
of evapotranspiration of 493.60 mm/days. In addition, the environmental conditions of the low-suitability area were as follows: an average precipitation of the wettest month of 114.43 mm and an average precipitation level of the driest month of 4.21 mm.

### 3.3. Current potential suitable habitat of *B. chinensis* and assessment

The most suitable area for *B. chinensis* was distributed on the eastern Qinghai-Tibet Plateau, on the Loess Plateau, in the Sichuan Basin, and in the Yunnan-Guizhou Plateau border region (Figure 5A). The potential suitable habitat of *B. chinensis* was fragmented, and the areas of high

suitability were distributed in southern Gansu, part of Sichuan, southern Yunnan, and southwestern Xizang (Figure 5B). The areas of moderate suitability were distributed in the border areas of Shaanxi, Qinghai, and Sichuan Provinces. The areas of low suitability were distributed in southern Shaanxi, eastern Qinghai, and southwestern Sichuan provinces. The total potential areas of unsuitable, low-suitability, moderate-suitability, and high-suitability habitats were 8,676,094 km<sup>2</sup>, 455,451 km<sup>2</sup>, 170,260 km<sup>2</sup>, and 116,111 km<sup>2</sup>, accounting for 92.12%, 4.84%, 1.81%, and 1.23% of the total area of China, respectively.

Sampling sites and species distribution modeling showed that *B. chinensis* was mainly distributed in eight provinces, which is of great significance for the conservation of *B. chinensis*. Sichuan



**Figure 4.** Importance of bioclimatic or environmental variables. **A** Jackknife test of the importance of 10 variables in the distribution of *B. chinensis*. **B** Response curves of the four vital variables.

**Table II** Statistical analysis of 10 bioclimatic or environmental variables in relation to suitability (mean  $\pm$  SD)

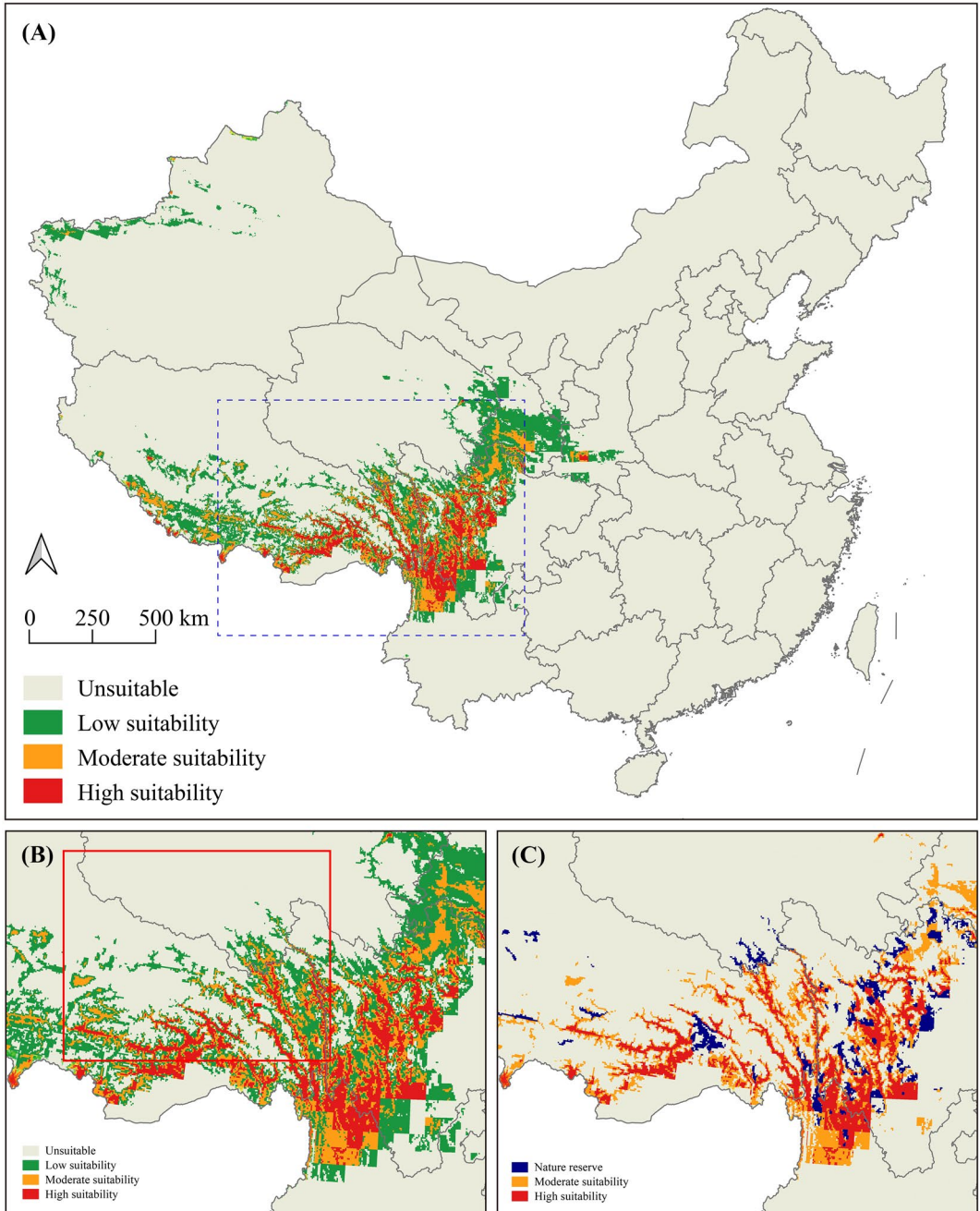
Variables	Value range for low suitability	Value range for moderate suitability	Value range for high suitability	Proposed mechanism
bio_03	34.06 ~ 51.60 (42.83 $\pm$ 5.09)	38.64 ~ 51.60 (45.12 $\pm$ 3.77)	41.96 ~ 51.60 (48.78 $\pm$ 2.81)	Affects the growth and distribution of food plants
bio_06	-18.74 ~ 0.91 (-8.91 $\pm$ 5.72)	14.87 ~ -3.06 (-8.97 $\pm$ 3.46)	-	Extreme values reduce nectar and pollen production by food plants
bio_10	-5.22 ~ 18.42 (6.60 $\pm$ 6.86)	3.36 ~ 12.55 (7.96 $\pm$ 2.68)	-	Affects the food-plant population, and outside activity
bio_13	17.97 ~ 210.90 (114.43 $\pm$ 56.12)	-	-	High values reduce foraging opportunities
bio_14	-4.90 ~ 13.33 (4.21 $\pm$ 5.31)	-	-	Affects the food-plant growth, and foraging opportunities
bio_15	24.69 ~ 114.51 (69.60 $\pm$ 26.03)	24.69 ~ 55.51 (40.10 $\pm$ 9.00)	-	Affects food-plant growth
bio_26	99.43 ~ 161.79 (138.95 $\pm$ 22.96)	99.43 ~ 145.43 (126.05 $\pm$ 15.51)	99.43 ~ 133.60 (116.74 $\pm$ 10.14)	Extreme values reduce nectar and pollen production by food plants
gdd	-540.30 ~ 1664.12 (561.91 $\pm$ 641.97)	-276.63 ~ 587.85 (432.24 $\pm$ 95.44)	-	Low values reduce nectar and pollen production by food plants, and reduce the seasonal window for population development
et0	162.00 ~ 1347.84 (754.92 $\pm$ 344.22)	162.00 ~ 825.19 (493.60 $\pm$ 193.35)	-	High values reduce nectar and pollen production by food plants
rds	4.36 ~ 17.92 (11.14 $\pm$ 3.93)	10.22 ~ 17.92 (14.07 $\pm$ 2.24)	16.20 ~ 17.92 (16.20 $\pm$ 1.01)	High values reduce foraging opportunities

Province has the widest distribution of high suitability, with an area of 50,677 km<sup>2</sup>, accounting for more than 11.13% of the province's total area. The second most high-suitability is in Xizang Province, with an area of 44,688 km<sup>2</sup> (3.99%). The third highest suitability is in Yunnan, with an area of 18,490 km<sup>2</sup> (5.65%). The area of high suitability in Shaanxi Province is 1,146 km<sup>2</sup> (2.04%). The area of moderate suitability in Gansu Province is 13,264 km<sup>2</sup> (3.19%). The area of low suitability was distributed in Qinghai, Xinjiang, and Ningxia Provinces. Among the sampling sites after 2000, one site in Yunnan Province was highly suitable, four sites in Gansu Province were highly suitable, and two sites in Xizang Province were less suitable. In Ningxia Province, one site had moderate suitability, five sites had low suitability, and one site was in an unsuitable area.

By calculating the degree of overlap between the potential suitability of *B. chinensis* and nature reserves in China, the results showed that 105,109 km<sup>2</sup> of suitable area is in the nature reserve, accounting for 14.18% of the total suitable area (Figure 5C). Located in the nature reserve, the area of high suitability was 16,128 km<sup>2</sup>, the area of moderate suitability was 29,670 km<sup>2</sup>, and the area of low suitability was 59,392 km<sup>2</sup>.

#### 4. DISCUSSION

In recent decades, bumble bees have declined, which has attracted widespread attention from scientists worldwide (Brown 2011; Goulson et al. 2015; Cameron and Sadd 2020). Cuckoo bumble bees face more significant threats than



**Figure 5.** Current distribution and conservation status of *B. chinensis*. **A** Potential habitat suitability of *B. chinensis*. **B** Detailed information on the distribution of the core region of *B. chinensis*. **C** The overlap between the main suitability of *B. chinensis* with nature reserves in China. Unsuitable (0–0.50), low suitability (0.50–0.75), moderate suitability (0.75–0.90), and high suitability (0.90–1.00).

their host bumble bees because of their unique physiological characteristics and biological habits (Antonovics and Edwards 2011; Lhomme and Hines 2019). In this study, the potential distribution of the cuckoo bumble bee *B. chinensis* was successfully determined by open-source software. Species distribution modeling revealed the current fragmentation distribution of this cuckoo bumble bee, which provided a basis for further research and conservation strategies.

In total, there were 34 sampling sites in our model (Figure 1). Although the sampling data were limited, the AUC value of the distribution model reached 0.977, the value of TSS was 0.620, and *F*-measures reached 0.529 which indicated that the model was “great” (Supplementary Table S1). In addition, many studies have shown that MaxEnt has higher performance than other SDMs and has lower uncertainty when using fewer occurrence records (Phillips et al. 2006; Pearson et al. 2007; De Marco and Nóbrega 2018). Therefore, the potential distribution results obtained by MaxEnt modeling and the geographical suitability results for *B. chinensis* were relatively reliable.

Four variables (minimum temperature of coldest month, growing degree days, isothermality, and mean temperature of the warmest quarter) were found to be the most important climate factors influencing the distribution of suitable habitat of the bumble bee *B. chinensis* (Figure 4). The moderately suitable climate for *B. chinensis* was characterized by a growing degree day value between  $-276.63$  and  $587.85/\text{day}$ , minimum temperatures higher than  $-14.87\text{ }^{\circ}\text{C}$ , and mean temperatures of the warmest quarter lower than  $12.55\text{ }^{\circ}\text{C}$ . We concluded that *B. chinensis* prefers low-temperature and humid areas, as observed in other bumble bees (Penado et al. 2016; Lhomme and Hines 2019; Streinzer et al. 2019). Extreme climate conditions are unsuitable for the bumble bee life cycle (Kerr et al. 2015; Rasmont et al. 2015). For example, extreme values of growing degree days, mean temperature of the warmest quarter, and minimum temperature of the coldest month will reduce nectar and pollen production by food plants. Moreover, low values of growing degree days also reduce the seasonal window for

population development. Extreme values of the mean temperature of the warmest quarter and rainy days also reduce foraging opportunities, as confirmed in previous studies (Williams et al. 2014; Hu et al. 2021).

The current suitable habitat of *B. chinensis* was fragmented, and the areas of high suitability were scattered in Yunnan, Sichuan, Xizang, Gansu, and Qinghai Provinces (Figure 5A). This may be caused by not only climate change but also other factors, such as human activity, habitat loss, introduced pathogens, invasive alien species, and pesticide use (Brown 2011; Goulson et al. 2015; Cameron and Sadd 2020). Human influences, such as urbanization, anthropogenic land reclamation, the substitution of agricultural land for wild grassland, and the construction of roads and railways, have reduced natural habitats to remnants of varying scales (Mader 1984; Baur and Erhardt 1995; Redpath et al. 2010; Nahid et al. 2020). This poses a threat to bumble bees by limiting the range over which bumble bees can move between patches of vegetation (Bhattacharyaa et al. 2003).

The decline in pollinators has prompted scientists to analyze the potential distribution and conservation status of bumble bees (Arbetman et al. 2017; Richardson et al. 2018; Naeem et al. 2019; Cameron and Sadd 2020). Compared with the 25 suitable areas of bumble bees in Naeem’s study, the suitable area of 24 species was larger than the suitable area of *B. chinensis*, and only the distribution of *B. longipennis* was smaller (Naeem et al. 2019). It is more difficult to compare the distribution of cuckoo bumble bees due to the special parasitic nature of *Psithyrus*. At present, the distribution of cuckoo bumble bees in Asia has not been predicted. However, it was reported that cuckoo bumble bees of *B. cornutus* (Frison), *B. turneri* (Richards), *B. expolitus* (Tkalcu), *B. rupestris* (Fabricius), *B. coreanus* (Yasumatsu), *B. bohemicus* Seidl, *B. skorikovi* (Popov), and *B. norvegicus* were present in the distribution areas of *B. chinensis* (An 2012; Huang and An 2018). Their potential distribution is still unclear, and the research method of this study could provide a reference for the investigation and research of these cuckoo bumble bees.

Because *B. chinensis* is a cuckoo bumble bee, it is important to investigate its host. Previous studies have suggested that *B. pyrosoma* is a potential host bumble bee species of *B. chinensis*. However, this has not been confirmed (Reinig 1935; Lhomme and Hines 2019). In our study, we determined the distribution of *B. chinensis* and compared it with the distribution of *B. pyrosoma* (Naeem et al. 2019; Hu et al. 2021). We infer that the bumble bee *B. pyrosoma* is not the host or that there may be more than one host of *B. chinensis*, which needs further investigation. In this study, the high suitability can be used as the primary investigation area of *B. chinensis* and its host bumble bee.

By analyzing the overlap degree between the suitability and nature reserves, we found that the current conservation situation of *B. chinensis* is not optimistic (Figure 5C). Most of the suitability (> 85%) is out of the nature reserves. The area of high suitability in nature reserves accounts for 2.17% of the total suitable area. Eight provinces where *B. chinensis* is distributed were evaluated as priority conservation and investigation areas. Among them, Sichuan and Xizang Provinces had the largest potential highly suitable areas, which should be prioritized for establishing conservation areas. In addition, *B. chinensis* was found in Ningxia during the 2019 sampling investigation, so the region should also be protected and further investigated.

In conclusion, the fragmented habitat of the cuckoo bumble bee *B. chinensis* was revealed by sampling sites and climate variables based on open-source software. Four vital bioclimatic or environmental variables, namely, the minimum temperature of the coldest month, growing degree days, isothermality, and mean temperature of the warmest quarter, were recognized as the most significant variables affecting the distribution of this species. Therefore, the conservation of *B. chinensis* should be strengthened in Yunnan, Sichuan, Xizang, Gansu, Qinghai, Xinjiang, Shaanxi, and Ningxia Provinces, especially in areas with high habitat suitability and suitable climate factors. In addition, due to the limited sampling data, further sampling is required in the future. The host of the bumble bee *B.*

*chinensis* should be investigated for further conservation.

## SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-022-00942-5>.

## ACKNOWLEDGEMENTS

We thank Jiaoyao Liu, Yaning Zhang, Biao Wang, Yuling Zhang, and Shiwen Zhang for their help with sample collection.

## AUTHOR CONTRIBUTION

Conceptualization: J. Huang and J. An. Methodology: X. Hu, J. Huang, and M. Naeem. Software: X. Hu. Validation: J. Huang and J. An. Formal analysis: X. Hu. Investigation: X. Hu, G. Ding, and Y. Li. Resources: J. Huang and F. Ma. Data curation: X. Hu, G. Ding, and J. An. Writing, original draft preparation: X. Hu. Writing, review and editing: M. Naeem, G. Ding, J. Huang, and J. An. Visualization: X. Hu and J. Huang. Supervision: J. Huang. Project administration: J. Huang and F. Ma. Funding acquisition: J. Huang and F. Ma. All authors have read and agreed to the published version of the manuscript.

## FUNDING

This research received funding in part by the biodiversity investigation, observation, and assessment program of the Ministry of Ecology and Environment of China, the Agricultural Science and Technology Innovation Program (CAAS-ASTIP-2021-IAR) and the China Agriculture Research System (CARS-44).

## DATA AVAILABILITY

Species occurrence data used in MaxEnt modeling are available upon request.

## CODE AVAILABILITY

Not applicable. We used open-source Maxent and QGIS software.

## DECLARATIONS

**Ethics approval** No approval of research ethics committees was required to accomplish the goals of this study because there was no experimental work on animals and all in-

formation was based on unregulated, preserved invertebrate species or publicly available data.

**Consent to participate and consent for publication** No consent to participate or consent to publish was needed since this study did not involve the participation of humans as research subjects.

**Conflict of interest** The authors declare no competing interests.

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