The potential distribution and dynamics of important vectors *Culex pipiens pallens* and *Culex pipiens quinquefasciatus* in China under climate change scenarios: An ecological niche modelling approach

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Abstract

BACKGROUND: Intense studies have been carried out on the effects of climate

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change on vector-borne diseases and vectors. *Culex pipiens pallens* and *Culex pipiens quinquefasciatus* are two medically concerned mosquito species in temperate and tropical areas, which serve as important disease-transmitting pests of a variety of diseases. The ongoing geographically expansion of these mosquitoes has brought an increasing threat to public health.

RESULTS: Based on mosquito occurrence records and high-resolution environmental layers, an ecological niche model was established to model their current and future potential distribution in China. Our model showed that the current suitable area for *Cx. p. pallens* is distributed in the central, eastern and northern parts of China, while *Cx. p. quinquefasciatus* is distributed in vast areas in southern China. Under future climate change scenarios, both species were predicted to expand their range to varying degrees and RCP 8.5 provides the largest expansion. Northward core shifts will occur in ranges of both species. Environmental variables which have significant impact on the distribution of mosquitoes were also revealed by our model.

CONCLUSION: Severe habitat expansion of vectors is likely to occur in the future 21st century. Our models mapped the high-risk areas and risk factors which needs to be paid attention. The results of our study can be referenced in further ecological surveys and will guide the development of strategies for the prevention and control of vector-borne diseases.

Keywords: *Culex pipiens pallens*, *Culex pipiens quinquefasciatus*, global climate change, ecological niche model, vector-borne diseases

1. Introduction

Due to the diversity and widespread distribution of vectors, vector-borne diseases are common threat to global public health since ancient times. The history of malaria can be traced back to 2700 BC in China and the first confirmed plague pandemic was in Europe since the sixth century.[1, 2] In modern history, dengue appeared in 1779 and Japanese encephalitis virus was first isolated in 1933.[3, 4] In recent years, outbreaks of emerging vector-borne diseases such as Zika have begun to occur.[5] Mosquito is one of the most common vectors that can transmit a variety of serious human and animal diseases, such as *Aedes aegypti* transmits dengue, *Culex tritaeniorhynchus* transmits Japanese encephalitis and *Anopheles gambiae* transmits malaria.[6-8] *Culex pipiens* complex, which is one of the most widely distributed mosquito species all over the world, has been considered as important vectors for many years.[9] The global spread of *Cx. pipiens* complex has been observed and was presumed to be caused by human activities and climate change.[10, 11] Therefore, we are facing an increasing risk of exposure to vector-borne diseases due to the spread of mosquitoes.

The taxonomy of *Cx. pipiens* complex has been considered as a complex problem because of its various subspecies.[12] In China, four subspecies of *Cx. pipiens* complex have been found: *Cx. p. pallens*, *Cx. p. quinquefasciatus*, *Cx. p. pipiens* and *Cx. p. molestus*. *Cx. p. pipiens* was only recorded to present in Beijing, Shenyang and northern Taiwan.[13, 14] And *Cx. p. molestus* exists only in limited areas of Xinjiang Uygur Autonomous Region.[15] *Cx. p. pallens* and *Cx. p. quinquefasciatus* are two most widely distributed subspecies of *Cx. pipiens* complex in China which are mainly medically concerned. *Cx. p. pallens* and *Cx. p. quinquefasciatus* are mainly distributed in northern and southern China respectively. And because of their habit of living in human settlements, they are known as the "Northern/Southern house mosquito".[16] They together served as important vector of West Nile fever and lymphatic filariasis.[17-19] In addition, these two species are also involved in the transmission of a range of human and animal diseases, such as Rift Valley fever, Zika, St. Louis encephalitis and Dog heartworm.[20-22] The monitoring and control of *Cx. pipiens* complex is of great importance to the pathogen detection and prevention of infectious diseases.

Ecological niche modelling is a widely accepted approach to predict potential distribution of species and epidemic diseases.[23-26] For the establishment of a presence-only ecological niche model, occurrence records of target species and environmental variables which are considered to be related to the survival activities of the species are needed. The geographical suitability of the target species can be calculated by the built-in algorithms of the model. Risk assessments of vector-borne diseases by modelling the distribution of vectors have been highlighted in many previous studies, such as the modeling of *Lutzomyia* for leishmaniasis, *Culex tritaeniorhynchus* for Japanese encephalitis, and *Aedes aegypti*/*Aedes albopictus* for dengue [27-29]. Predicting the potential distribution of disease vectors is helpful to carry out more targeted and efficient vector monitoring and pathogen detection work. It can also guide the implementation of controlling programs of vector-borne diseases.[30, 31]

Vector-borne diseases are sensitive to changes of climate and land-use. Climate variation has an effect on the social behavior of vector populations, such as warmer winters result in northward range expansions of tropical vectors.[32, 33] And land-use changes transform natural environment which may create or destroy habitats for mosquitoes, such as unplanned urbanization provides human blood source and artificial containers for urban mosquito vectors.[34, 35] Based on the increasingly serious situation for prevention and control of vector-borne diseases, it is essential to take out a better understanding on the possible geographical dynamics of vector species in response to climate change. We therefore adopted an ecological niche modelling approach to predict the current potential range of *Cx. p. pallens* and *Cx. p. quinquefasciatus* in China, based on documented occurrence records and high-resolution environmental variables including climate and land-use factors. The Inter-governmental Panel on Climate Change, known as IPCC, unites global climate research communities to model the possible global climate change. The future climate predictions in the fifth assessment report (AR5) of the IPCC were simulated based on the "Representative Concentration Pathways (RCPs)".[36] Future (2006 – 2100) simulations based on these RCPs enabled projections for future niches to be made for the future 21st century.

2. Methods

2.1 Mosquito occurrence data

Mosquito occurrence data which include larvae and adult collections in China were obtained from two sources. Firstly, a comprehensive and systematic literature retrieval was performed on Web of Science, Scopus, ScienceDirect, PubMed and

CNKI (Chinese national knowledge infrastructure). Articles which contain geographical coordinates of mosquito capture sites were adopted. For records which do not provide coordinates but have detailed geographic descriptions, using Google Map to get coordinates. Occurrence records before 1990 and without clear location descriptions were not included. In this source, 427 records of *Cx. p. pallens* were collected from 173 published articles, and 233 records of *Cx. p. quinquefasciatus* from 101 articles. The second source was the Global Biodiversity Information Facility (GBIF) database (https://www.gbif.org/). GBIF provides global distribution information of a large number of species about where and when a species presents. No *Cx. p. pallens* records in China were recorded on GBIF, but 12 records of *Cx. p. quinquefasciatus* were obtained. Since our study would be performed under the resolution of 2.5 arcmin (approximately 5km × 5km), records within one grid cell were considered as one point. After the filtering of occurrence records, the final mosquito occurrence database consists of 375 unique points of *Cx. p. pallens* and 208 unique points of *Cx. p. quinquefasciatus* (Fig 2) (Details of occurrence records in Table S1). To avoid the possible confounding caused by spatial stratified heterogeneity (SSH), we tested Wang's q-Statistic by GeoDetector (http://www.geodetector.cn/).[37, 38] County level occurrences were paired with integer codes representing the provincial level administrative regions to which they belong.[39, 40] The q-Statistic test indicates no significant SSH exists in samples of *Cx. p. pallens* (q = 0.430; p = 0.304) and *Cx. p. quinquefasciatus* (q = 0.319; p = 0.177).

Fig 1. Flow chart of analyses in this study.

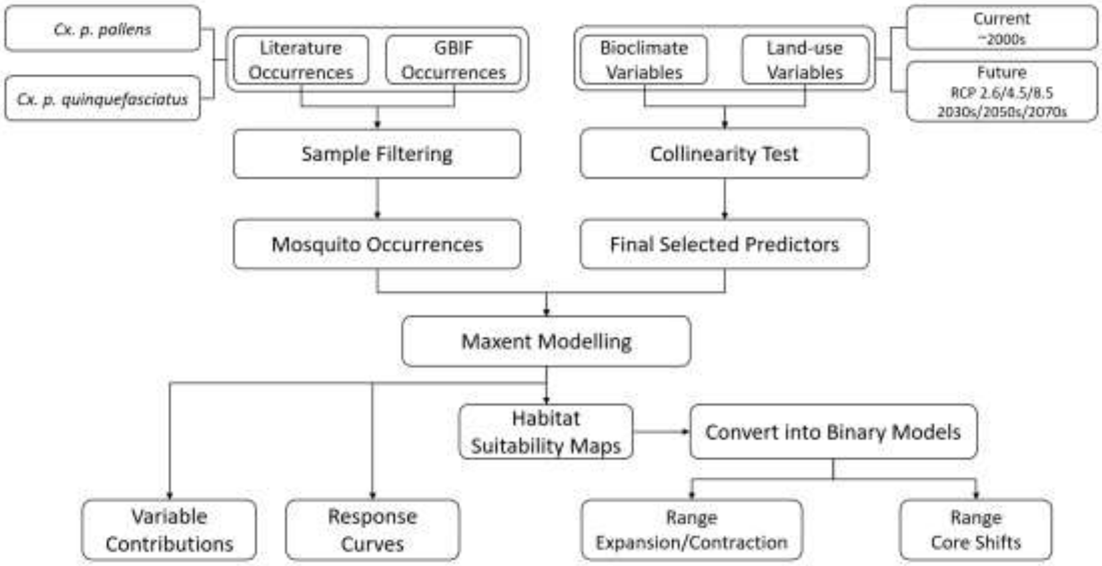
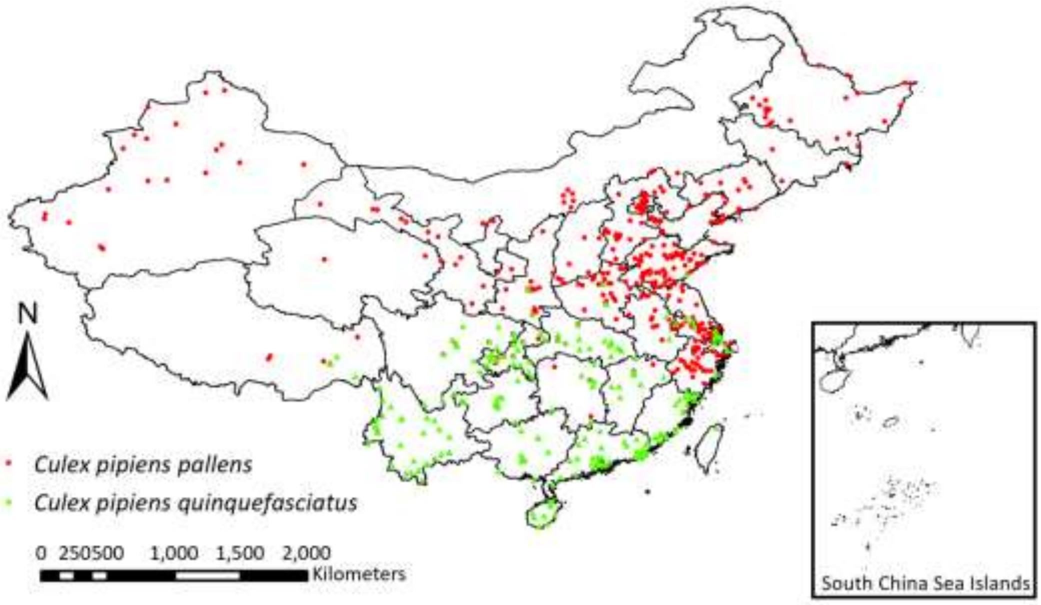


Fig 2. Occurrence records of *Cx. p. pallens and Cx. p. quinquefasciatus* in China.



2.2 Environmental variables and data processing

Nineteen bioclimate variables and twelve land-use variables were introduced as environmental variables into the model (Table 1). Data for current climate conditions were downloaded from WorldClim (http://worldclim.org/version1). In this dataset, bioclimate variables reflecting global temperature and precipitation conditions were provided as the current (1960-1990) baseline for future (2030s, 2050s and 2070s) projections. Data for future climate conditions were downloaded from the database of Climate Change, Agriculture and Food Security (CCAFS) (http://ccafs-climate.org/). The RCPs describe assumptions about the possible emission of greenhouse gases (GHG) in the future 21st century.[41] Five GCMs (Global Climate Models) of BCC-CSM 1-1, BNU-ESM, LASG-FGOALs-g2, CanESM2 and CSIRO-Mk3.6.0 were used in our study (Table 2). These GCMs are the most commonly used models for simulating the climate change in China, and three of them were developed by Chinese institutions.[42-45] The final results are the average of the predictions across these five GCMs. To account for the uncertainty of global climate change, we chose RCP 2.6 as the minimum emission scenario, RCP 4.5 as the medium, and RCP 8.5 as the maximum. Both current and future variables have a high resolution of 2.5 arcmin (approx. 5km × 5km).

Land-use variables were downloaded from the Land-Use Harmonization (LUH2) database (http://luh.umd.edu/index.shtml). The LUH2 dataset is part of the World Climate Research Program Coupled Model Intercomparison Project (CMIP6). Projections of fractional global land-use patterns at 0.25°x 0.25° resolution from 850 to 2100 were provided in this dataset. Future land-use conditions are also driven by RCP scenarios.

Variable	Description	Source	Data Range	Spatiotemporal Resolution
Bio 1	Annual mean temperature			
Bio 2	Mean diurnal range			
Bio 3	Isothermality (Bio 2/Bio 7)			
Bio 4	Temperature seasonality (Standard deviation*100)			
Bio 5	Maximum temperature of the warmest month			
Bio 6	Minimum temperature of the coldest month			
Bio 7	Temperature annual range (Bio 5-Bio 6)			
Bio 8	Mean temperature of the wettest quarter			
Bio 9	Mean temperature of the driest quarter			
Bio 10	Mean temperature of the warmest quarter	WorldClim CCAFS	Global	1960~1990; 2030s~2070s 2.5 arcmin
Bio 11	Mean temperature of the coldest quarter			
Bio 12	Annual precipitation			
Bio 13	Precipitation of the wettest month			
Bio 14	Precipitation of the driest month			
Bio 15	Precipitation seasonality (Coefficient of variation)			
Bio 16	Precipitation of the wettest quarter			
Bio 17	Precipitation of the driest quarter			
Bio 18	Precipitation of the warmest quarter			
Bio 19	Precipitation of the coldest quarter			
C3ann	C3 annual crops			
C3per	C3 perennial crops			
C3nfx	C3 nitrogen-fixing crops			
C4ann	C4 annual crops			
C4per	C4 perennial crops			
Primf	Forested primary land			
Primn	Non-forested primary land	LUH2	Global	850~2100 0.25 degree
Secdf	Potentially forested secondary land			
Secdn	Potentially non-forested secondary land			
Pastr	Managed pasture			
Range	Rangeland			
Urban	Urban land			

Table 1. Variables used in the model.

ID	GCMs	Developer
1	BCC-CSM 1-1	Beijing Climate Center, China Meteorological Administration, China
2	BNU-ESM	The College of Global Change and Earth System Science, Beijing Normal University, China
3	LASG-FGOALs-g2	Institute of Atmospheric Physics, Chinese Academy of Sciences, and Tsinghua University, China
4	CanESM2	Canadian Centre for Climate Modelling and Analysis, Canada
5	CSIRO-Mk3.6.0	Australian Commonwealth Scientific and Industrial Research Organization, Australia

Table 2. GCMs used in the model.

We extracted bioclimate and land-use variables with the same scenarios (RCP 2.6, RCP 4.5 and RCP 8.5) and time (2030s, 2050s and 2070s). Land-use layers were resampled to the same resolution as bioclimate layers of 2.5 arcmin using the Nearest Neighbour method and all layers were cropped to the geographical area of China. All operations were accomplished in ArcGIS 10.2 (ESRI Inc., Redlands, CA, USA).

In order to eliminate the collinearity between variables, we use Pearson correlation coefficient to judge the correlation between each pair of variables ($|r|\geq 0.70$).[46-48] In each pair of correlated variables, one of them needs to be removed. To determine which one has weaker predictive power, we pre-run the model for both species with each single variable. The one with lower AUC value was removed. Furthermore, variables with AUC<0.7 in one-variable models were also removed, because they have weak predictive power. Moreover, reducing the number of predictors in SDMs is conducive to improve the accuracy of the model and reduce the risk of over-fitting.[49, 50] Finally, two different sets of predictors were separately obtained for two mosquito species.

2.3 Model training

Maxent (version 3.4.1), a java-based software for ecological niche modelling was used to establish the model (http://biodiversityinformatics.amnh.org/open_source/maxent/). Maxent is one of the most widely used niche modelling methods, because of its outstanding predictive performance in comparative studies on various modelling methods.[51-53] We set 25% of the occurrence points as test points (randomly selected by the program), and the remaining 75% as training points.[54] The average logistic output of 10 replicates for each model were taken as the final predictions.[55]

Sampling bias is a common problem in species distribution modeling.[56] Sampling locations are usually biased toward areas which are conveniently accessed. To counter the sampling bias, "pseudo-absences" with the same spatial bias as the presence points are recommended to introduced into the model.[57-59] To this end, SDMtoolbox v2.2 (http://sdmtoolbox.org/), a python-based tool for ArcGIS, was used to create a Gaussian Kernel Density of sampling localities to address the bias.[60, 61] A bias grid which up-weights presence points with fewer neighbours in the geographic landscape was generated. In order to find the optimal spatial distance used to quantify region of spatial bias, we conducted several experimental runs within 0-50 km away from presence points. The distance setting which provided the best prediction accuracy was found by maximizing the TSS (True skill statistic) value (results were shown in Fig S1).[62, 63] And 10,000 background points was recommended for Maxent to get accurate predictions.[64]

2.4 Model Evaluation and Interpretation

The receiver operating characteristic curve (ROC) was used to evaluate the model performance. A greater area under the curve (AUC) value (0 ~ 1) indicates a better predictive performance.[65]

To understand the role of environmental variables in the modelling, “Percent contribution (PC)” and “Permutation importance (PI)” were widely used evaluation indicators for Maxent.[66-68] “Percent contribution” is defined as the increase contributed by the corresponding variable in regularized gain when the training algorithm runs. “Permutation importance” is defined as the resulting drop in training AUC when values of the corresponding variable are randomly permuted. Both indicators were normalized to percentages. A higher PC or PI can both indicate the importance of the corresponding variable to the model. Response curves of one-variable models were generated by the model which reflect the relationship between environmental variables and the habitat suitability.

2.5 Estimating habitat changes between current and future

Binary models are widely used to convert continuous suitability map into either-or presence/absence map for practical applications and model evaluations. To estimate the area of suitable habitat for mosquitoes, “Maximum sensitivity plus specificity” probability threshold, was applied to generate binary models. This threshold has been widely used in modelling studies and considered as one of the best thresholds which can provide the most accurate predictions.[63, 69-71] Grids with logistic output greater than the threshold are considered as “Suitable” and otherwise as

"Unsuitable". We compared the habitat in future scenarios with the current and quantified the extent of habitat change (expansion or contraction) based on binary models. To explore the direction of core distributional shifts between current and future ranges, we summarized the distribution to a single point, the centroid of the niche.[60, 72, 73] The centroids of the simulated niches were calculated by averaging the latitude and longitude of all "Suitable" grids in binary models.[74]

3 Results

3.1 Current distribution of *Cx. p. pallens* and *Cx. p. quinquefasciatus*

The modelling results are shown in Figs 3 and 4. The AUC value is 0.918 ± 0.015 in *Cx. p. pallens* model, and 0.943 ± 0.012 for *Cx. p. quinquefasciatus.*

Fig 3. Modelled habitat suitability of *Cx. p. pallens* in China.

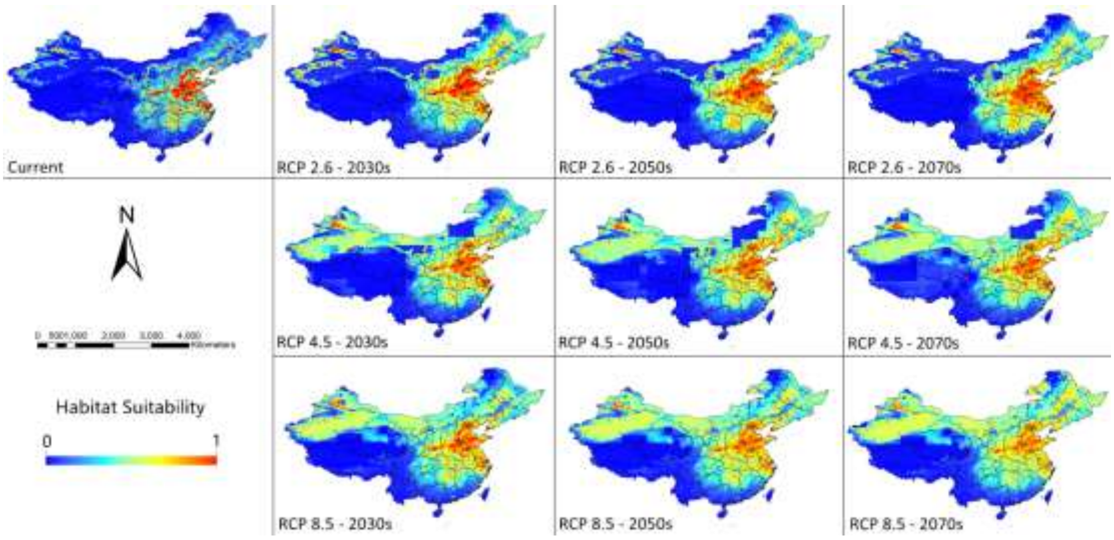
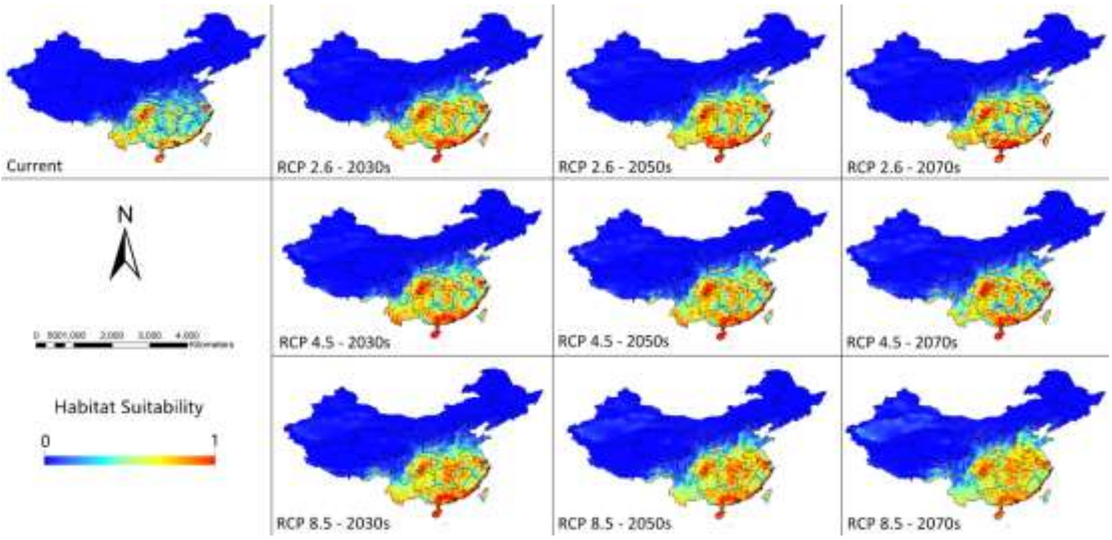


Fig 4. Modelled habitat suitability of *Cx. p. quinquefasciatus* in China.



The current habitat suitability of *Cx. p. pallens* was modelled to be high in central, northern and eastern China. The most concentrated highly suitable habitats for *Cx. p. pallens* were in Hebei, Shandong, Henan, Anhui, Jiangsu and Zhejiang. All northern provinces were predicted to have some areas suitable for *Cx. p. pallens* survival. Although few occurrences presented in southern China, Sichuan, Chongqing, Guizhou, Hunan and Jiangxi were predicted to have certain suitability for the survival of *Cx. p. pallens*.

Currently, *Cx. p. quinquefasciatus* was modelled to occupy a wide ecological niche range in areas of southern China. Areas of southeastern coast and southwestern China show the highest suitability. Among inland provinces, Hubei, Hunan, Jiangxi, Anhui and even parts of Shaanxi and Henan were likely to have some suitable habitats.

3.2 Habitat change under future climate change scenarios

Changes of suitable habitat was predicted to occur in both species under the trends of future climate change. Under different climate change scenarios, the habitat suitability will change to varying degrees. With the increase of hypothetical emissions of GHG, habitat suitability of *Cx. p. pallens* was also predicted to increase in China. Under RCP 4.5 and 8.5, large areas of Xinjiang are predicted to become moderate suitable for *Cx. p. pallens.*

The habitat suitability of *Cx. p. quinquefasciatus* is expected to increase in northern areas and the high suitability areas tend to shift eastward and expand in the southeast China. Areas with high suitability in eastern Sichuan, Chongqing, Hubei, Hunan, Anhui, Jiangxi, southern Jiangsu, northern Zhejiang, Guangdong, Guangxi will continue to increase suitability and area. It is noteworthy that the habitat suitability in a small part of southeastern Tibet are expected to increase.

The expansion and contraction of ranges of both species are more intuitive in binary models (Figs 5 and 6). *Cx. p. pallens* was predicted to expand its range mainly in northern regions, including Xinjiang, Inner Mongolia, northeast provinces and even parts of Qinghai. And its current range will continue to expand and little contractions may occur (Table 3). RCP 8.5 causes the largest expansion and least contraction. There will be likely no change in the southern boundary of *Cx. p. pallens* habitat.

For *Cx. p. quinquefasciatus*, large areas of new habitat will be established in all central and southeastern provinces. Its northern boundary is predicted to extend northward at least into Henan and Shandong (RCP 2.6 and 4.5), and even into Hebei (RCP 8.5). However, some contractions in Yunnan were modelled under all future scenarios.

Fig 5. Predicted changes in modelled range of *Cx. p. pallens* under current and future climate scenarios. Binary models were generated based on "Maximum sensitivity plus specificity" threshold (0.218).

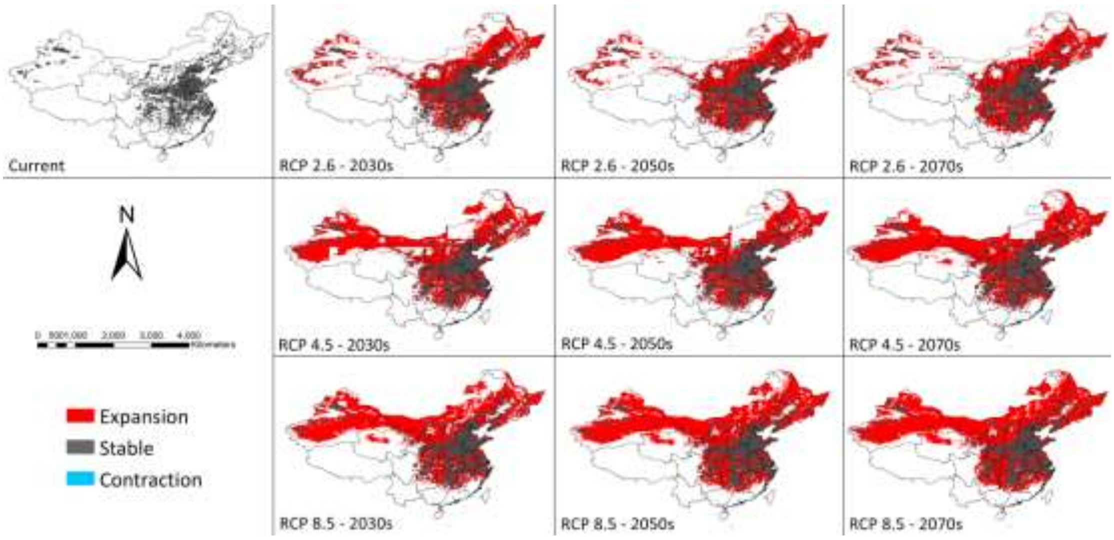
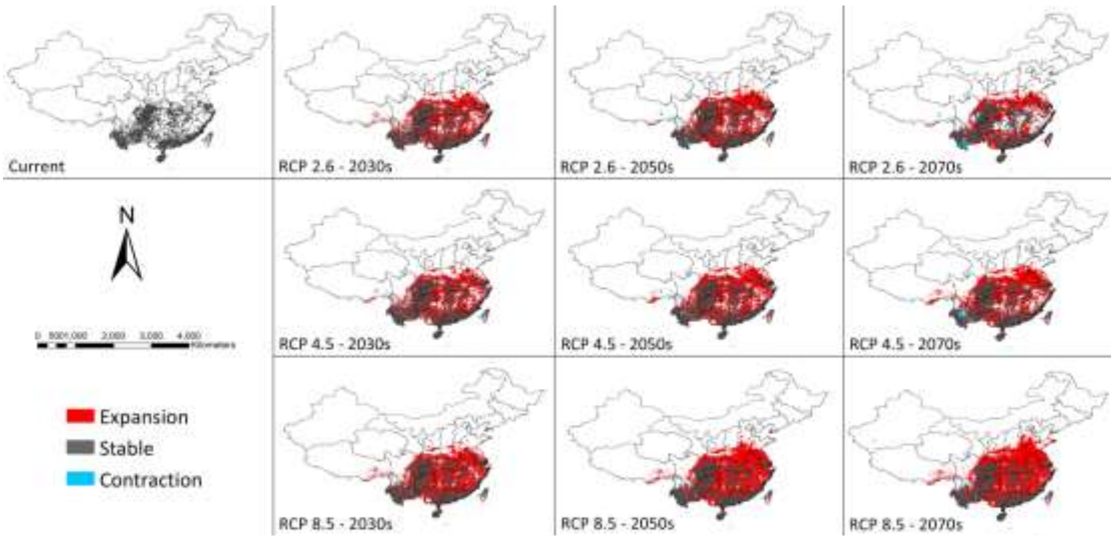


Fig 6. Predicted changes in modelled range of *Cx. p. quinquefasciatus* under current and future climate scenarios. Binary models were generated based on "Maximum sensitivity plus specificity" threshold (0.294).



Species	RCPs	Area of modelled range / thousand km^2								
		2030s			2050s			2070s		
		Stable	Expansion	Contraction	Stable	Expansion	Contraction	Stable	Expansion	Contraction
Cx. p. pallens	RCP 2.6	1592.76	1874.78	13.76	1591.27	2123.09	15.26	1572.51	2120.02	34.01

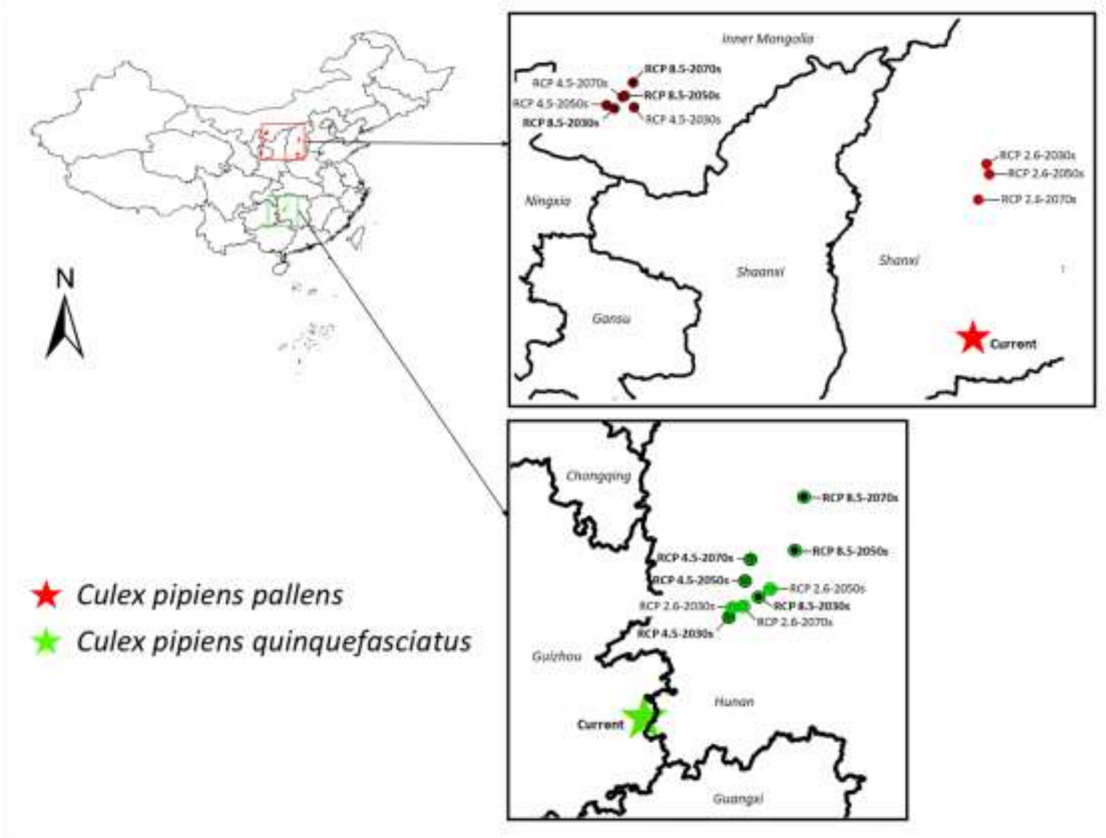
	RCP 4.5	1597.65	2836.26	8.87	1586.30	3013.66	20.23	1587.74	3230.69	18.78
	RCP 8.5	1603.36	3234.26	3.17	1603.71	3691.39	2.81	1603.41	3892.28	3.12
Cx. p. quinquefasciatus	RCP 2.6	1231.13	915.10	1.90	1209.54	976.41	23.50	1152.10	773.70	80.93
	RCP 4.5	1225.45	867.42	7.58	1221.63	1040.43	11.41	1207.56	1071.86	25.47
	RCP 8.5	1228.09	1081.04	76.92	1222.41	1319.97	10.62	1218.97	1490.06	14.07

Table 3. Estimated area change of modelled range of both species.

3.3 Range shifts between current and future models

The change of centroids reflects the directional shift of future ranges (Fig 7). Under different climate change scenarios, the direction changes of *Cx. p. pallens* are simulated to be quite different. Its range is expected to shift northward in Shanxi under RCP 2.6 and northwestward into Inner Mongolia under RCP 4.5 and 8.5. For the range of *Cx. p. quinquefasciatus*, the current centroid is in Guizhou and is expected to shift northeastward into Hunan under all scenarios.

Fig 7. Centroid changes between current and future models.



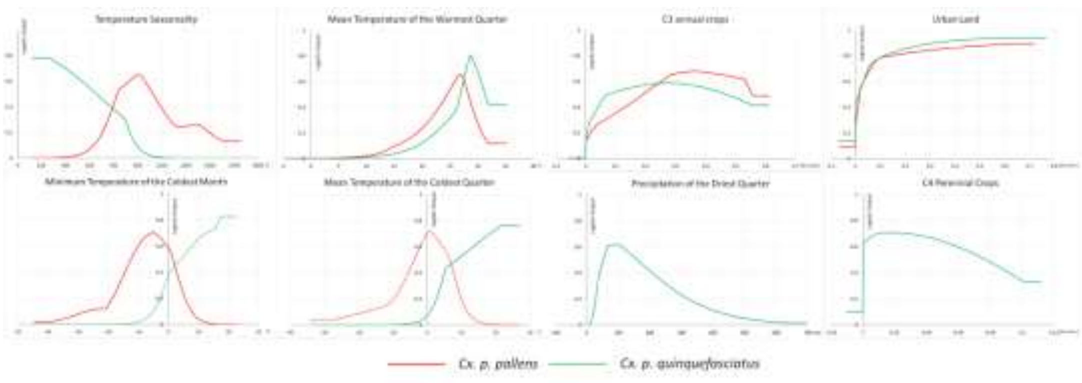
3.4 Variable contributions

Variables used in the final models were shown in Table 4, as well as the "Percent contribution" and "Permutation importance" of each set of variables. Different variables were considered as important predictors in models for two species. The response curves of important predictors were shown in Fig 8. The different trends of response curve of the same variable in different models will help us understand the appropriate environmental requirements of different species.

	Cx. p. pallens		*Cx. p. quinquefasciatus*	
	PC (%)	**PI (%)**	**PC (%)**	**PI (%)**
Temperature Seasonality	9.70	19.77	3.46	0.77
Minimum Temperature of the Coldest Month	1.33	11.48		
Mean Temperature of the Warmest Quarter	2.26	5.46	1.27	1.39
Mean Temperature of the Coldest Quarter			12.41	62.17
Precipitation Seasonality			1.43	2.12
Precipitation of the Wettest Quarter	0.35	1.24		
Precipitation of the Driest Quarter			28.06	2.31
Precipitation of the Warmest Quarter			1.09	2.12
C3 Annual Crops	13.39	36.26	1.34	7.70
C3 Perennial Crops	9.08	2.10	0.39	1.35
C3 Nitrogen-fixing Crops	0.42	1.57	0.49	3.27
C4 Annual Crops	1.26	2.33	1.20	2.28
C4 Perennial Crops			22.72	0.17
Potentially Forested Secondary Land			0.97	1.97
Managed Pasture	1.13	2.54	1.85	1.84
Rangeland			2.64	4.11
Urban Land	61.07	17.25	20.69	6.41

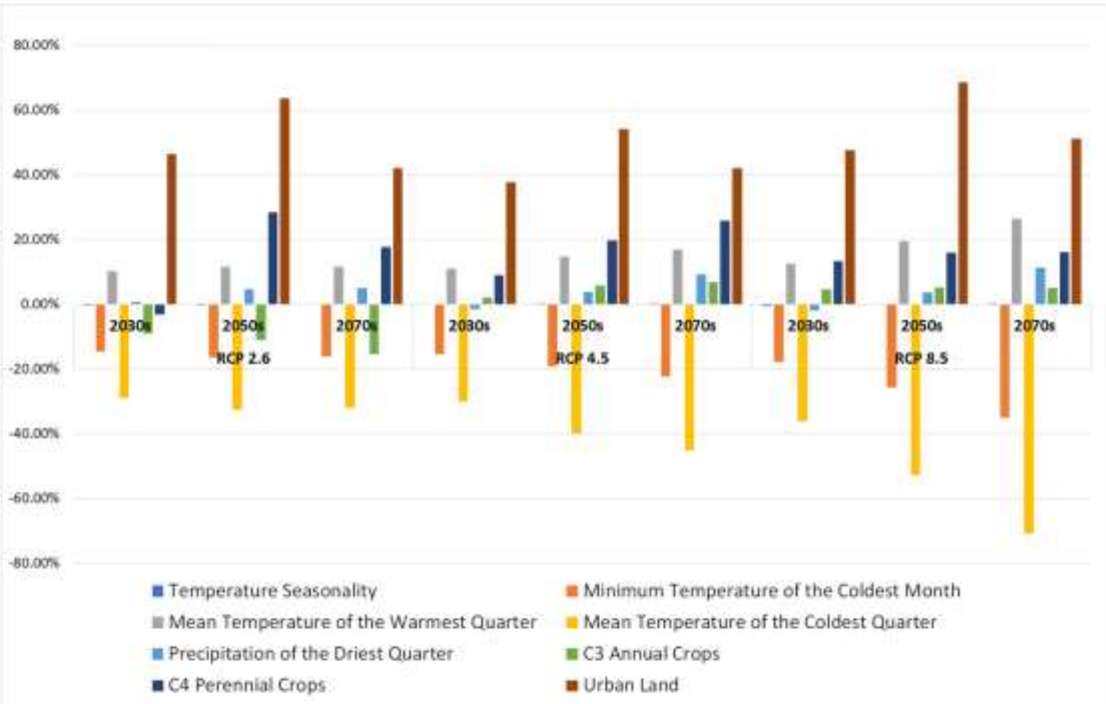
Table 4. Variable contributions in each model. PC: Percent contribution; PI: Permutation importance.

Fig 8. Response curves of variables with greater contribution.



The projected changes in the above predictors were shown in Fig 9. We can observe the differences in the degree of environmental variations between RCPs and time periods. Among bioclimate predictors, both summer and winter temperatures are expected to rise significantly and the degree of rise is basically positively related to the increase in emission assumptions. However, there is nearly no projected changes in “Temperature seasonality”. Minor variations may occur in “Precipitation of the driest quarter”. Among land-use predictors, moderate variation of “C3 annual crops” and “C4 perennial crops” may be observed and “Urban land” presents the largest increase in future scenarios.

Fig 9. Projected changes in important predictors. It should be noted that the values of “Minimum temperature of the coldest month” and “Mean temperature of the coldest quarter” were negative. Therefore, their negative growth under future climate change represents an increase in their values, which means a warmer winter.



4. Discussion

The surveillance and control of common disease-transmitted vectors, such as mosquitoes, is of great importance for the prevention and control of vector-borne infectious diseases. According to the recommendation of WHO, one of the most effective strategies for eliminating vector-borne infectious diseases is to control the vectors or intermediates host of the pathogens.[75] However, the vast territory is the major challenge to the development of comprehensive vector detection in China. The first provincial regulation on vector control in China was issued in Liaoning province in 2002. In order to ensure the scientific, standardized and unified monitoring work, the Ministry of Health of China issued the first version of "National Vector Monitoring Program" in 2005. According to our models, targeted vector monitoring and verification of *Cx. pipiens* complex can be carried out to guide a more efficient and purposeful pathogen detection.

All climate change scenarios lead to varying degrees of habitat expansion. The assumption of RCP 8.5 provides both the largest expansion in two species (Table 3). Under the trend of climate warming, vast areas in northern China are likely to become new habitats for *Cx. p. pallens* in the future (Fig 3 and 5). *Cx. p. quinquefasciatus* is expected to increase its suitability on most areas of the current basis and expand its habitat northward, reaching as far as Hebei (Fig 4 and 6). The main direction of range shift of *Cx. p. pallens* is northward (RCP 2.6) or northwestward (RCP 4.5 and 8.5) while *Cx. p. quinquefasciatus* is northeastward (Fig 7). The shift direction of *Cx. p. pallens* under RCP 2.6 is quite different from other RCPs. This may find its cause in the projected changes of predictors (Fig 9). "C3 annual crops" is projected to decrease under RCP 2.6, while increase under RCP 4.5 and 8.5. Overall, the degree of centroid shift is positively related to the severity of the climate change hypothesis. Both species have a tendency to spread northward under future climate changes. It is suggested that the monitoring of mosquito vectors should be strengthened in northern China.

Due to the different environmental adaptability of these two species, they occupy different geographical areas. A rough description of the geographical distribution of these two mosquito species was mentioned in a previous overview, which is roughly consistent with our modeling results.[12] However, compared with our study, the northern boundary of the *Cx. p. quinquefasciatus* distribution was described to be too far north, such as include Shandong into the current range of *Cx. p. quinquefasciatus*. And another study in 1995 pointed out that 30°N was the theoretical line of demarcation for these two species by means of regression.[15] Although the claimed demarcation line falls within the range predicted by our model, the reference value of its results is no longer significant. Both the sampling occurrences and our modelling results presented the possible habitat overlap of these two species in central regions of China, and the area which may serve as suitable habitats for both species shows the trend of further expansion in the future. The deficiency of our study is that, to accurately measure the niche overlap, the SDM-based method (such as Maxent adopted in our study) was pointed out to be an inappropriate method.[76] Future investigations and studies on their niche overlap and interactions are expected to carry out in central regions of China.

The response curves reflect the different environmental requirements of these two mosquito species (Fig 8). According to response curves of Bio 4 (Temperature seasonality), these two species show different dependence on temperature conditions. When the annual temperature has a large temperature seasonality (standard deviation), *Cx. p. pallens* has significantly higher suitability than *Cx. p. quinquefasciatus.* In other words, it has the ability of adapting cold winters. Their response to extreme low temperature was also shown in Bio 6 (Minimum temperature of the coldest month) and Bio 11 (Mean temperature of the coldest quarter). These two variables are highly correlated. For a more direct comparison, additional response curves (dashed lines) were obtained by interchange these two variables to establish additional models. *Cx. p. pallens* still holds high suitability when the lowest winter temperature and average winter temperature are below 0°C, but the suitability of *Cx. p. quinquefasciatus* is very low in this case. *Cx. p. quinquefasciatus* prefers higher winter temperature. The overwintering ability of *Cx. p. pallens* has been highlighted in previous studies.[77, 78] It has been proved that *Cx. p. pallens* are able to enter an adult diapause characterized by arrested ovarian development, enhanced stress tolerance, and elevated lipid stores, but *Cx. p. quinquefasciatus* lacks the ability.[79] Therefore, *Cx. p. quinquefasciatus* are distributed in southern China, which is closer to the tropics and provides temperature conditions that are less variable throughout the year and warm winters. However, the response curves of Bio 10 (Mean temperature of the warmest quarter) shows the adaptability of these two species to extreme high temperatures. The curve of *Cx. p. quinquefasciatus* has a higher peak and suitability than *Cx. p. pallens.* The optimum temperature of *Cx. p. quinquefasciatus* is predicted as 28.7°C and for *Cx. p. pallens* was 26.7°C. The adaptability of these two mosquito species to high temperatures were studied in a previous study.[80] It was pointed out that, compared with *Cx. p. pallens*, *Cx. p. quinquefasciatus* has a higher egg hatchability, insemination, and longevity at high temperatures. This is the reason why *Cx. p. quinquefasciatus* can live in tropical areas. According to the response curve of Bio 17 (Precipitation of the driest quarter), southern areas with adequate precipitation in dry season are favorable to *Cx. p. quinquefasciatus.* Drought is unfavorable for mosquito survival because water is necessary for the hatching of eggs and the development of mosquitoes.[81] But excessive rainfall can be detrimental to its development, through wash-out of eggs in water containers, especially for *Cx. p. quinquefasciatus*, which is a kind of well-known house mosquito.[82] Water containers in human settlements are important habitats for house mosquitoes, both *Cx. p. quinquefasciatus* and *Cx. p. pallens* can get steady and sufficient water supply. This is also the reason why they showed similar response curve on "Urban land". Another reason is that both species are common mosquitoes in urban areas which feed on human blood.[83] Land-use variables showed similar trends in response curves and "C3 annual crops" and "C4 perennial crops" were those with greater contribution. For mosquitoes, a certain amount of vegetation is needed for their sugar feeding and agricultural irrigation is also a kind of water supply, but too much a fraction of croplands means fewer urban lands. The above is our simple understanding of the effects of environmental variables on the survival of these two mosquito species according to the response curves. However, these effects should be interpreted with caution. Our model can only roughly reflect the relationship between mosquitoes and environmental variables. Further ecological research is required to clarify the specific role of these environmental variables in the survival and social activities of these two mosquito species.

Our study is novel in our purpose on modelling both the current and future potential distribution of the two important vectors *Cx. p. pallens* and *Cx. p. quinquefasciatus* in China under multiple climate change scenarios. As mentioned above, previous estimates of the geographical distribution of these two vectors in China were based on estimates derived from observations that were not comprehensive enough in time or space. Our study provided a more comprehensive review of mosquito occurrence records. Based on the latest available high-resolution datasets of climate and land-use conditions and future predictions, the niche shift and overlap of these two vectors in China was modelled for the first time. Our model improves our understanding of their ecological status in China. Our findings can serve as a reference for more efficient monitoring of mosquitoes and detection of vector-borne disease pathogens under the trends of global climate change. The prevention and control of many vector-borne diseases may benefit from our study.

Our study on the distribution prediction of *Cx. p. pallens* and *Cx. p. quinquefasciatus* in China by means of an ecological niche modelling approach still has some limitations. The "suitable habitat" predicted by our model was actually the ideal ecological niche which meets the environmental conditions for the species to live. And these environmental conditions are only those that were introduced into our model. Due to various dispersal limitations, such as human activities, geographical barriers and interspecific competitions, such niches are highly unlikely to be filled by the target species. So we should keep in mind that the introduction of more environmental and socioeconomic variables reflecting survival limitations of the species is always necessary to develop a more precise and realistic model.

It is recommended to conduct continuous monitoring of mosquitoes in high-risk areas predicted by our model. On the one hand, it can be used to verify the accuracy of the model, on the other hand, the addition of further occurrence data will help to improve the model. Based on our study, if sufficient occurrences and time-series environmental data are available, a seasonal dynamic model is expected to be developed to investigate the different distribution pattern among seasons. That may help to explore the timing to carry out mosquito control effort.

5. Conclusion

Based on mosquito occurrence records and high-resolution environmental layers representing climate and land-use conditions, the current and future potential distribution of *Cx. p. pallens* and *Cx. p. quinquefasciatus* in China was modelled using an ecological niche modelling approach. The current models performed well in representing the distribution of observed occurrence records. In the future 21^{st} century, both species were assumed to have the possibility to establish new habitats as the climate changes. Several environmental variables were revealed to play an important role on mosquito survival. Our predictions have strategic implications for the control of vectors and prevention of vector-borne diseases.

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Supporting information

Table S1. Mosquito occurrences database.

Appendix: Supplementary materials.

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