Research Article

Received: 11 December 2023 Revised: 1 June 2024 Published online in Wiley Online Library: 25 June 2024

(wileyonlinelibrary.com) DOI 10.1002/ps.8257

Forecasting habitat suitability and niche shifts of two global maize pests: *Ostrinia furnacalis* and *Ostrinia nubilalis* (Lepidoptera: Crambidae)

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Abstract

BACKGROUND: *Ostrinia furnacalis* (ACB) and *Ostrinia nubilalis* (ECB) are devastating pests of the agricultural crop maize worldwide. However, little is known about their potential distribution and niche shifts during their global invasion. Since long-term selection to past climate variability has shaped their historical niche breadth, such niche shifts may provide an alternative basis for understanding their responses to present and future climate change. By integrating the niche unfilling, stability, and expansion situations into a single framework, our study quantifies the patterns of niche shift in the spatial distribution of these two pests during the different periods.

RESULTS: Our results show that the overall suitable habitats of ACB and ECB in the future decrease but highly and extremely suitable habitat will become more widespread, suggesting these two insects may occur more frequently in specific regions. Compared with Southeast Asia and Australia, the ACB niche in China exhibited expansion rather than unfilling. For ECB, initial niches have a tendency to be retained in Eurasia despite there also being potential for expansion in North America. The niche equivalency and similarity test results further indicate that niche shifts were common for both ACB and ECB in different survival regions during their colonization of new habitat and their suitable habitat changes during the paleoclimate were associated with climatic changes.

CONCLUSIONS: These findings improve our understanding of the ecological characteristics of ACB and ECB worldwide, and will be useful in the development of prevention and control strategies for two insect pests worldwide.

Supporting information may be found in the online version of this article.

Keywords: niche shifts; *Ostrinia furnacalis*; *Ostrinia nubilalis*; ecological niche models; habitat suitability

1 INTRODUCTION

The niche conservatism hypothesis assumes that most species that colonize a new habitat still tend to remain within their native niches due to long-term adaptation to the initial climatic conditions.[1,2] However, habitat suitability is changing in response to climate change and reduced habitat for many species, such as insects, mammals, birds and amphibians.[3-5] Moreover, increasing evidence indicates that some species of concern can rapidly adapt to new habitats through niche shifts, resulting in significant harm to biodiversity, agriculture, and human health.[6,7] Therefore, understanding the effects of niche shifts will improve predictions of response to future climate change through adaptive evolution and support increased sustainability of agricultural management practices.[8]

When biological interactions are very strong or climate change occur frequently, many economically important pests have changed niches in ways that differ markedly from their initial niches in order to match their specific requirements.[9] A useful conceptual framework for understanding changes in the ecological relationship between species and their environment is (i) unfilling (climate conditions in invasion range not overlapped with the native niche), (ii) expansion (climate conditions available in invasion range but not in the native range), and (iii) stability (the portion of native climatic niche overlapping the invasive climatic niche).[10] However, how pest species have evolved to adapt to a new habitat by changing niche is not well understood. Considering the intricate interplay between agricultural pests' adaptability to climate change and biotic interactions, which encompass factors such as temperature, precipitation, shifts in ranges, and host

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resources, ecological niche models (ENMs) offer a robust approach for assessing niche disparities and forecasting potential habitat suitability.[11]

As closely related species within the Lepidoptera order, *Ostrinia furnacalis* (Asian corn borer, ACB) and *Ostrinia nubilalis* (European corn borer, ECB) are members of the *O. nubilalis* species group, primarily distinguished by the morphology of the male genitalia, as described in Yang *et al*. (2021, p. 830, Clade III in Fig. 1).[12] Studies have documented that ACB and ECB exhibit considerable phenotypic diversity, which is likely pivotal for their adaptation to varied environmental conditions.[13,14] Notably, geographic populations exhibit variation in life history traits, such as critical day length (CDL) and post-diapause emergence times, which correlate with latitude.[15,16] ACB has effectively expanded beyond climatic zones, colonizing the Indochina Peninsula, the South Asian subcontinent and Oceania,[17,36] whereas ECB, originally endemic to Europe, has become a significant maize pest in North America following its accidental introduction in the early 20th century.[18,19] Furthermore, recent investigations have revealed the co-occurrence of both pests in the Yili Kazak Autonomous Prefecture of Xinjiang, China.[20,21] Consequently, ACB and ECB represent exemplary models for investigating niche shifts, attributed to their extensive distribution patterns and demonstrated capacity for environmental adaptation.[14,22]

The ACB and ECB may have evolved strong dietary convergence due to global maize introduction.[23] Currently, the dietary generalism of these two pests and their ability to withstand relative extremes of temperature and altitude are believed to have enabled them to persist in a diverse array of niches in North America and Eurasia, including rainforest, savanna, temperate forest, and high-altitude montane regions.[14,15,20] A high rate of ACB infestation causes heavy damage in corn and other crops in south-east Asia and Australia, and a 10–30% corn yield reduction in China and the Philippines.[24] ECB has been responsible for maize yield losses exceeding $1 billion annually in North America.[25] Environmental and genetic drivers of variation in the number of generations per year (voltinism) are well documented.[26,27] Overall, these patterns suggest that ACB and ECB could have the capacity to change their spatial correlations with environmental factors by shifting their distributional ranges and fundamental niches they historically occupied.[28,29] However, critical evidence remains missing on niche shift and whether that contributes to survival and adaption of these two species in various environmental conditions.

Here, we aim to characterize future distribution changes and niche shifts for ACB and ECB within native and invaded ranges under alternative climate scenarios. We developed ENMs by integrating occurrence records with critical bioclimatic variables to forecast the global habitat suitability of these two insect pests. Subsequently, we examined the degree of niche shifts within their current geographical distributions. Moreover, we employed the conceptual framework of niche unfilling, stability, and expansion to elucidate the observed variations in niche divergence among the distinct geographical populations of these pests. Ultimately, we derived preliminary estimates of their global potential distributions and delineated maps of ecological habitat suitability for the species. This effort furnishes a comprehensive theoretical support for predicting the niche dynamics of agricultural pests on a global scale.

2 MATERIALS AND METHODS

2.1 Spatial aggregation analyses of occurrence data

To identify the effects of climate change on two pests in the primary agricultural production areas worldwide, original occurrence records of ACB and ECB in respective survival ranges were collected and interpreted by searching online database and various collections. First, we searched the occurrence records of ACB from the Global Biodiversity Information Facility (largest-scale biodiversity database of biological collections and various sources for species distributional data in the world, GBIF, https://www.gbif.org/),[30] mainly including crop production sites of Southeast Asia and Australia. To increase data collection of ACB records, we also obtained detailed occurrence data of ACB in China through field surveys during the summer 2017–2023. For ECB, known occurrence records in the Eurasia and North America were downloaded from GBIF.[31] All records with detailed geographic information of these two insects were generated independently (Supporting Information, Table S5 and S6). To avoid potential sampling bias, occurrence records at geographical distances <50 km were removed using the 'thin' function of the R package 'spThin' in R 4.2.0.[32] The remaining occurrence records of both species were mapped using ArcGIS 10.8.

2.2 Correlation analysis of bioclimatic variables

Bioclimatic variables from 1970 to 2000 at a resolution of 2.5 arcmin were downloaded from WorldClim 2.1 (http://www.worldclim.org/) that mainly contains 20 bioclimatic variables derived from monthly temperature and precipitation values. Subsequently, to predict the future habitat suitability and distribution of two pests, two different representative concentration pathways (RCPs) (RCP 2.6: the selected pathway declines to 2.6 W m^{-2} by 2100; RCP 8.5: Rising radiative forcing pathway leading to 8.5 W m^{-2} by 2100) from the MICR5 dataset were selected for the two periods (2050s: average for 2041–2060; 2070s: average for 2061–2080) (WOS: 000274394300028).[33] In addition, the last interglacial (LIG), last glacial maximum (LGM) and mid-Holocene bioclimatic variables from the WorldClim 2.1 were used to describe paleoclimate change. To minimize multi-collinearity among bioclimatic variables, a Pearson's correlation coefficient for pairwise comparison was calculated in the R package 'stats'. One of the two variables with a correlation coefficient $|r| > 0.70$ was randomly removed.

2.3 Ecological niche modeling

2.3.1 *Modeling approach*

Ecological niche models (ENMs) were implemented in the present study to assess niche disparities and forecast potential habitat suitability,[11] because they can incorporate the complex interplay between species adaptability to climate change and biotic interactions, such as temperature, precipitation, and shifts in ranges and host resources. We adopted the commonly used maximum entropy algorithm (MaxEnt 3.4.4) to construct ENMs due to its robust predictive performance, flexible hyperparameter settings, accessibility, and simple operation,[34] which had been used in many previous studies to forecast potential geographical distribution by comparing the similarities of habitats between occurrences and background environments under settled constraints.[35-38]

2.3.2 *Model settings and evaluations*

The R package 'ENMeval'[39] was used to calibrate the MaxEnt model by setting different combinations of featured classes (FCs: linear (L), quadratic (Q), product (P), threshold (T) and hinge (H)) and regularization multiplier (RMs).[40] RMs were set from 0.2 to 2 at 0.2 intervals. Seven combinations of FCs, including 'L,' 'LQ,' 'LQP,' 'H,' 'LQH,' 'LQHP,' and 'LQHPT,' were used.[40] To explore the best model, a total of 70 models (including the default auto-feature model) totally compared based on the Akaike's information criterion (AIC). Other parameter settings were as follows: multiplier = 1, maximum iterations = 5000, convergence threshold = 0.0001 and maximum number of background points = 10, 000. To avoid overfitting of redundant bioclimatic variables, the lowest values for the differences between the training and testing areas under the curve (AUC.diff) and 10% training omission rate (or.10p) were also determined.[41] In order to quantify the discrimination accuracy of ENMs, 25% of the occurrence records were used as the test set while the remaining 75% were used as the training set randomly with a 10-fold cross-validation approach.[42] Model performance was typically judged as reliable when the area under receiver operating characteristic curve (AUC) > 0.8, true skill statistics (TSS) > 0.7 and continuous Boyce index (CBI) > 0.7.[43]

2.4 Habitat suitability prediction and analysis

The suitable habitats of ACB and ECB were converted to raster format, ranked and extracted using the world administrative division map using species distribution models (SDM) Tools within ArcGIS 10.8. The suitable habitats were then classified into four types at equal interval classification based on the minimum training presence logistic threshold (MTP): unsuitable habitat suitability (0–0.25), moderate habitat suitability (0.25–0.50), high habitat suitability (0.50–0.75) and extreme habitat suitability (0.75–1.00).[44]

2.5 Niche shift analysis

For ACB, niches were compared by dividing the thinned occurrence records into the three separate ranges, including Southeast Asia, China and Australia. For ECB, niches compared native range (Eurasia) and invaded range (North America). To quantify the niche shifts, we set the minimum convex polygons formed by a range of 1° around the occurrence records within each range as buffer zones and randomly selected background points at 30 times the number of occurrences within each buffer zone.[45,46] Then, the selected bioclimatic variable information of all occurrence points and background points was extracted using the R package 'rgdal'.[47] Next, the selected bioclimatic variable information was generated into a 100 × 100 two-dimensional space and correlation circles of contribution by environmental principal component analysis (PCA-env) shared between the native and invaded ranges.[46] Finally, the smoothed densities of occurrences and background environments were then projected along the same two principal component axes for a robust comparison of native and invaded niches.[48]

In addition, niche equivalency and similarity tests were used to estimate whether the two pests were distinctively shifted in their

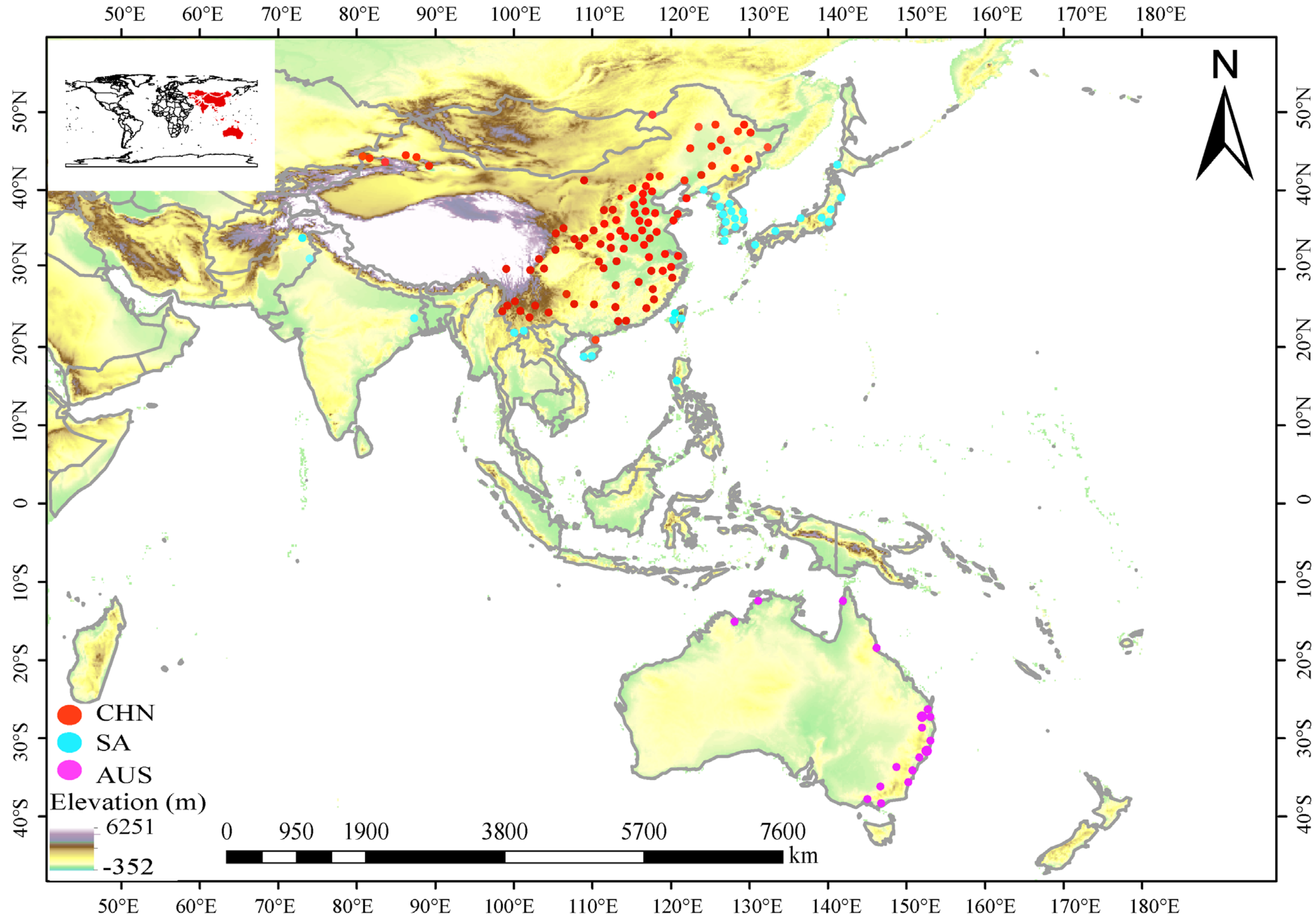

Figure 1. Map showing the occurrence records of *Ostrinia furnacalis* (ACB) in Southeast Asia (SA), China (CHN), and Australia (AUS).

respective native and invaded ranges. The niche equivalency test investigates the degree of overlap for species occurrence points when were pooled and reassigned to both the native and invaded ranges. The niche equivalency was estimated based on the metrics of Schoener's *D* and Warren *et al.*'s *I*.[49] Next, observed values of Schoener's *D* and Warren *et al.*'s *I* statistics were compared to 100 pseudoreplicates to produce a null hypothesis. $P < 0.05$ indicates the null hypothesis of niche unequivalency was rejected.[50] The values of two metrics were used to quantify the degrees of overlap between the native and invaded ranges, ranging from 0 (no overlap) to 1 (complete overlap).[50] Meanwhile, the similarity test was conducted to evaluate whether the degree of overlap of the observed niche is higher than the overlap between the observed niche in native range and a randomly selected niche in an invaded range after 100 repeats. The invaded niches were determined as more similar to the native niches than expected if the comparison is statistically significant ($P < 0.05$).[48,50] The same workflow was used to depict niche shifts between the native and invaded populations of both pests along each single bioclimatic variable, and the proportions of niche expansion, stability, and unfilling were estimated. The above processes were performed in R using the 'ecospat' package.[51]

3 RESULTS

3.1 Occurrence data thinning and bioclimatic variable selection

After spatial thinning to include only points at least 50 km apart, 145 and 358 evenly spread points were determined in major crop growing regions worldwide for habitat suitability modelling and niche shift analysis for ACB and ECB, respectively. In general, the georeferenced occurrence points of thinned occurrence records represent the currently known distribution areas of these two species (Figs 1 and 2). For ACB, bio2 (Mean Diurnal Range), bio4 (Temperature Seasonality), bio7 (Temperature Annual Range), bio11 (Mean Temperature of Coldest Quarter), bio13 (Precipitation of Wettest Month) and bio15 (Precipitation Seasonality) were used to construct ENMs (Supporting Information, Table S1 and Fig. S1). For ECB, bio1 (Annual Mean Temperature), bio3 (Isothermality), bio6 (Min Temperature of Coldest Month), bio9 (Mean Temperature of Driest Quarter), bio12 (Annual Precipitation), bio13 (Precipitation of Wettest Month), bio14 (Precipitation of Driest Month), bio17 (Precipitation of Driest Quarter) and bio19 (Precipitation of Coldest Quarter) were applied for habitat suitability modelling and climatic niche analysis (Supporting Information, Table S1 and Fig. S2).

3.2 Distribution modelling performance and evaluation

For ACB, the metrics were produced by various combinations of FCs and RMs and are depicted in Fig. 3. Based on AIC, we ultimately determined the best combination as FCs = LQH and RMs = 0.8, with the smallest evaluation metrics of delta.AIC = 0. The best metrics were generated with AUC.diff.avg = 0.0121, AUC.val.avg = 0.9403 and or.10p.avg = 0.1304, indicating that overfitting and complexity were effectively reduced. In general, our results showed that the selected model with random sampling successfully predicted the potential distribution of ACB with

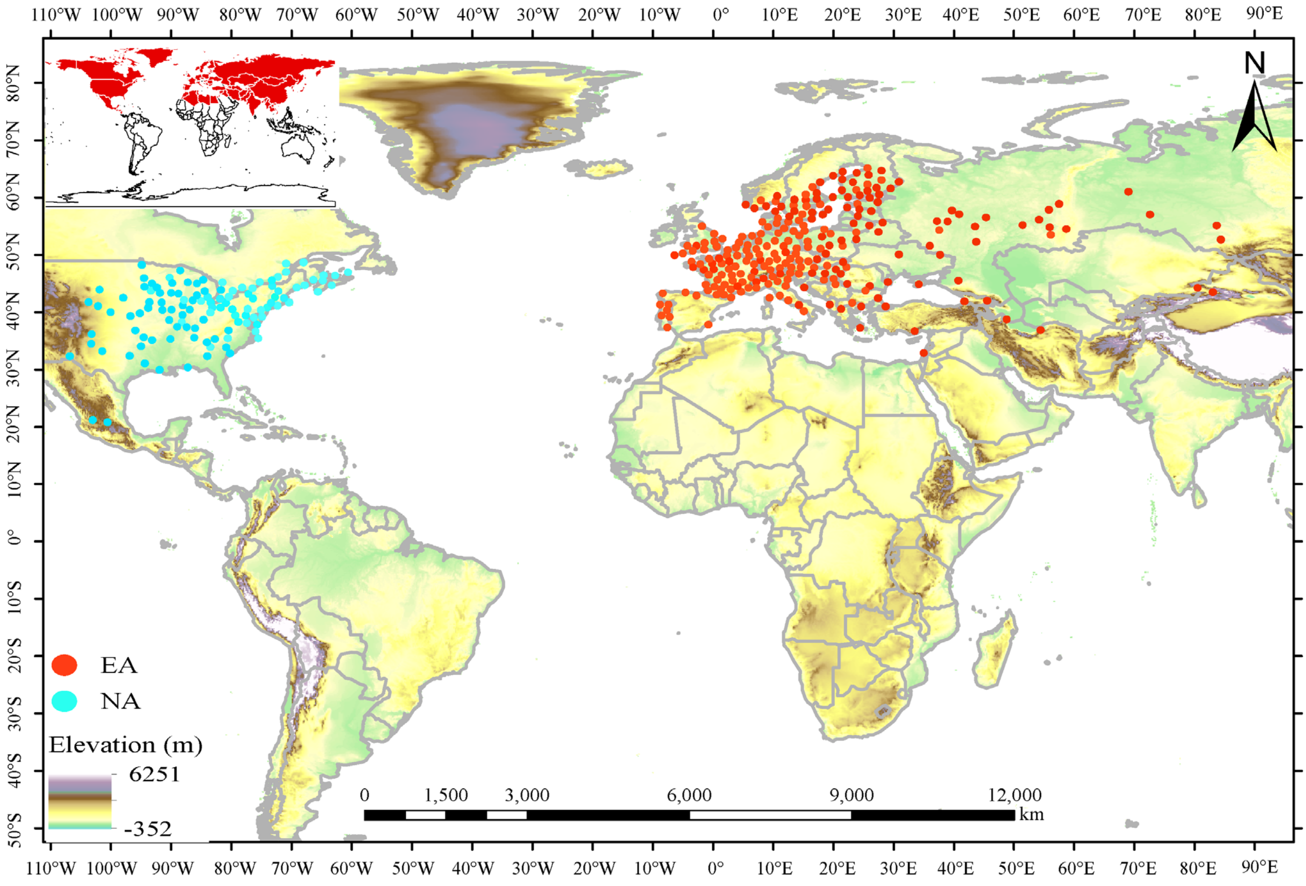

Figure 2. Map showing the occurrence records of *Ostrinia nubilalis* (ECB) in in Eurasia (EA) and North America (NA).

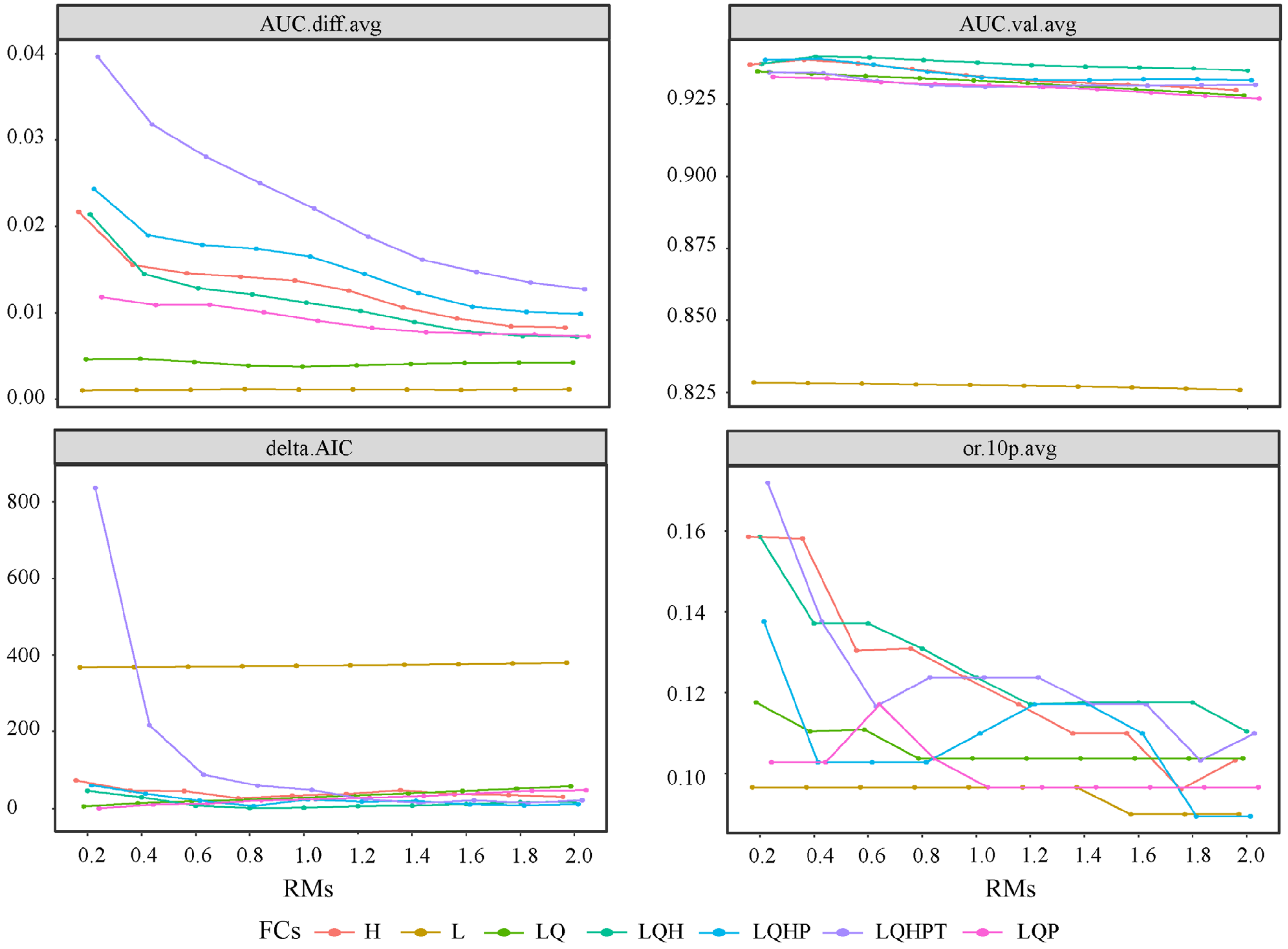

Figure 3. The results of MaxEnt model optimization for *Ostrinia furnacalis* (ACB) using different combinations of regularization multipliers (RMs) and feature classes (FCs).

highly reliable AUC values of 0.920, TSS of 0.909 and CBI of 0.718 (Supporting Information, Table S2). For ECB, we selected the optimal combination with FCs = LQH and RMs = 1.0 (the value of evaluation metrics of delta.AIC = 0). In addition, evaluation metrics of AUC.diff.avg = 0.0028, AUC.val.avg = 0.9517, and or.10p.avg = 0.1354 were determined in the best model (Fig. 4). Similarly, the optimized model with random sampling enabled to predict the potential distribution of ECB with high accuracy AUC values of 0.944, TSS of 0.801 and CBI of 0.895 (Supporting Information, Table S2). These results showed that the best model obviously reduced the overfitting of the distribution records for ACB and ECB, indicating that the model output was characterized by high prediction accuracy.

3.3 Habitat suitability prediction analysis

The ranges of suitable habitat for ACB and ECB worldwide are shown in Figs 5 and 6. For ACB, the highly and extremely suitable habitat are mainly distributed in the eastern coastal regions of China and tend to spread to the southeast. Additionally, Japan, the Korean Peninsula and the southeast of Australia were also major suitable habitat (Fig. 5(b)). Compared with the present, overall suitability habitat areas will decrease by 195.17–276.47 × 100^2 km^2 in the future (Table 1), which mainly includes moderately and extremely suitable habitat (Supporting Information, Table S3). In particular, the highly suitable areas steadily remained. By contrast, the unsuitable habitat increased by varying degrees under the different climate scenarios (Table S3). For ECB, the highly and extremely suitable habitats in North America were mainly distributed in the middle and eastern coastland (Fig. 6(b)). On the other hand, suitable habitat spanned from the littoral areas of the Mediterranean to the Far-eastern areas of Eurasia (Fig. 6(b)). The contracted suitable habitat formed an area of 6.75–51.68 × 100^2 km^2 besides the 2070 (RCP 2.6) (Table 2). However, the moderately suitable habitat areas remained and even increased under the different climate scenarios (Supporting Information, Table S3).

In addition, the overall suitable habitat for ACB decreased from the LIG to LGM (Fig. 5(a)), especially in moderately and extremely suitable habitat. By contrast, the highly and extremely suitable habitats for ACB rapidly increased from the LGM to the mid-Holocene (Supporting Information, Table S3). Overall suitable habitat areas for ACB gradually concentrated from the mid-Holocene to the present (Fig. 5(a)). For ECB, the overall suitable habitat decreased from the LIG to the mid-Holocene beside the unsuitable habitat (Fig. 6(a) and Supporting Information, Table S4). From the mid-Holocene to the present, the highly and extremely suitable habitat in North America for ECB increased markedly (Fig. 6 (a)). Our predicted results show that the potentially suitable

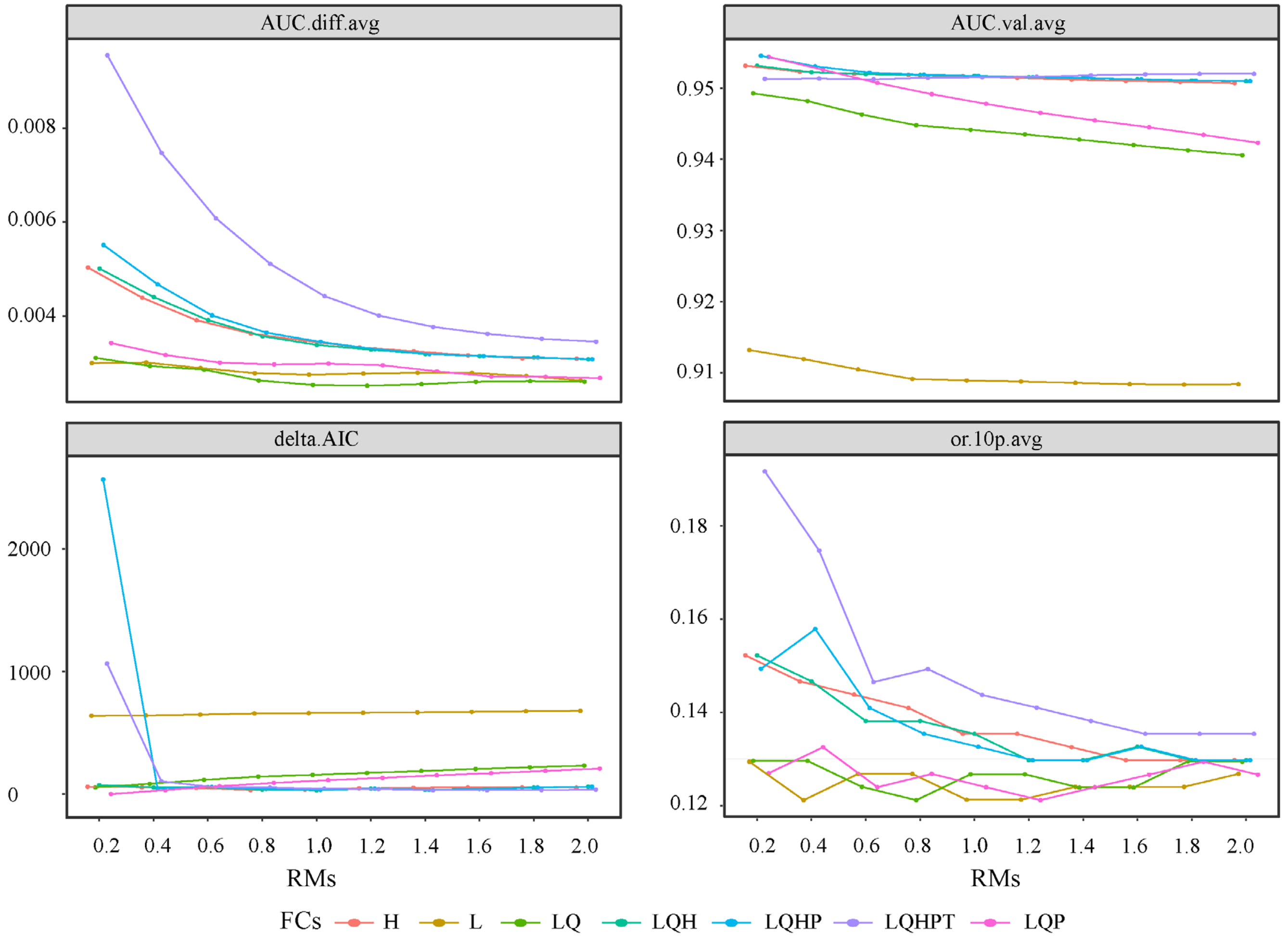

Figure 4. The results of MaxEnt model optimization for *Ostrinia nubilalis* (ECB) using different combinations of regularization multipliers (RMs) and feature classes (FCs).

habitat of the two species increased and became more concentrated over several millennia in response to environment or climate change.

3.4 Niche shift analysis

Niche shift analysis is shown in Fig. 7(a), (b). The first two principal components totally explain 74.71% and 87.29% of the original environmental variance for ACB and ECB, respectively. Furthermore, the selection of bioclimatic variables was determined based on the contribution loadings. For ACB, the bioclimatic variables which contribute the most to the model performance were bio4, bio7, bio11 and bio13 (Fig. 7(a)). For ECB, the most contributing bioclimatic variables were bio12, bio6, bio17, and bio3 (Fig. 7(b)). Our results indicate there are considerable differences in the climate preferences for different geographical populations of the two species. In addition, although niche unfilling was high between China and Australia, ACB experienced various degrees of niche expansion during colonization to a new habitat (Fig. 7(c)). For ECB, the niche of Eurasia populations shows a more obvious expansion than in the North America (Fig. 7(d)). In addition, the overlap results of the two species indicate that very limited niche overlaps are observed between the different distribution ranges (Table 3).

The ACB's climatic niches in Southeast Asia and China ($P = 0.1584$), Southeast Asia and Australia ($P = 0.4455$), China and Australia ($P = 0.4851$) and the ECB's climatic niches in Eurasia and North America ($P = 0.7426$) were dissimilar in terms of similarity test results (Supporting Information, Figs S3a, S3b), indicating that the colonization to new survival ranges resulted in different climate preferences from those of the original populations. On the other hand, the lack of significant results for the equivalency tests of the two insect pests suggests that there was major distinction between native and invaded niches (Fig. S3a, S3b). Overall, these findings indicate that the niches of these two species have undergone niche shifts during their adaptations to a new habitat.

4 DISCUSSION

Insects have evolved special adaptive mechanisms to survive in various environmental conditions.[52] Understanding the interactions between pests and future climate change is vital for developing strategies for pest control. Moreover, increasing evidence suggests that some species may undergo niche shifts during the colonization.[53,54] For example, a niche shift analysis of *Anoplophora glabripennis* and *Anoplophora chinensis* suggested differ-

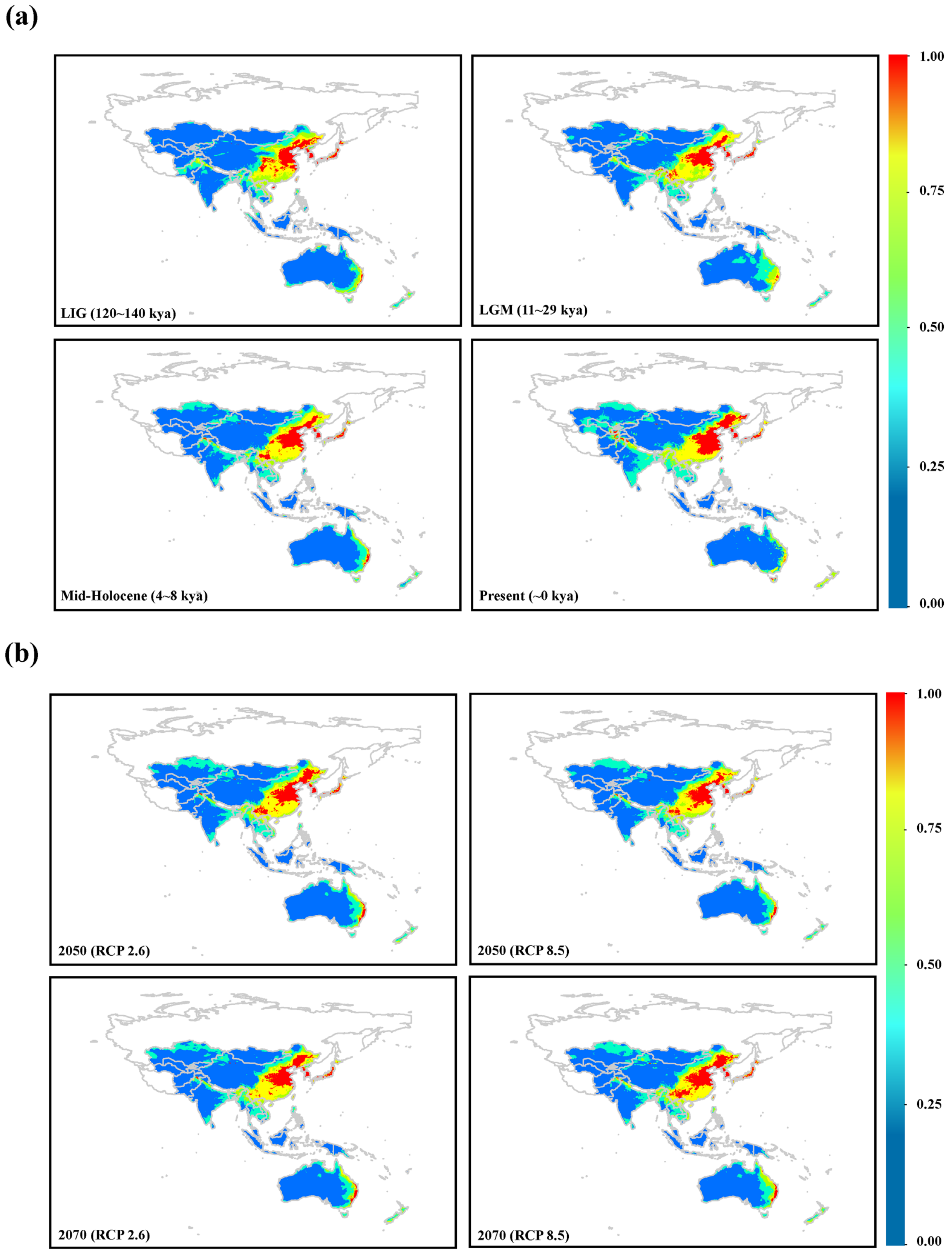

Figure 5. (a) Species distribution models of *Ostrinia furnacalis* (ACB) for historical (mid-Holocene, 4~8 kya; last Glacial Maximum (LGM), 11~29 kya; last Interglacial (LIG), 120~ kya) and present (~0 kya). (b) Species distribution models of ACB predicted in the 2050s and 2070s under RCP 2.6 and RCP 8.5 scenarios. Warmer colors indicate higher suitability of occurrence as predicted by MaxEnt. The base maps are from Standard Map Service website.

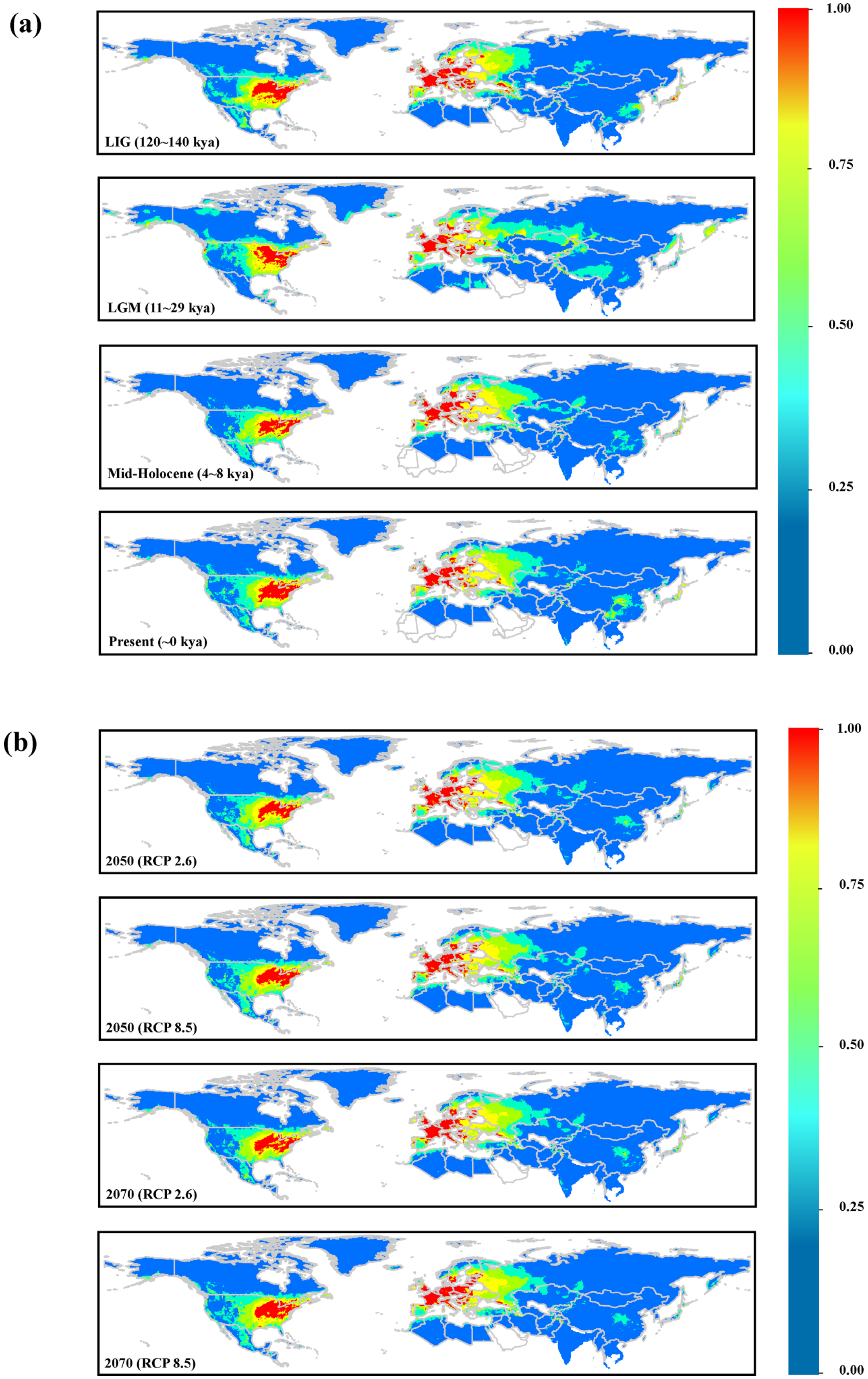

Figure 6. (a) Species distribution models of *Ostrinia nubilalis* (ECB) for historical (mid-Holocene, 4~8 kya; last Glacial Maximum (LGM), 11~29 kya; last Interglacial (LIG), 120~ kya and present (~0 kya)). (b) Species distribution models of ECB predicted in the 2050s and 2070s under RCP 2.6 and RCP 8.5 scenarios. Warmer colors indicate higher suitability of occurrence as predicted by MaxEnt. The base maps are from Standard Map Service website.

Table 1. Predicted suitable habitat area changes of *Ostrinia furnacalis* (ACB) from the current to future climatic scenarios

	ACB			
	Area change (100 $^{-2}$ km^{2})			
Climate scenarios	No change	Contraction	Expansion	Total
Currently–2050 (RCP 2.6)	660.77	371.05	112.61	−258.44
Currently–2050 (RCP 8.5)	656.83	374.98	98.51	−276.47
Currently–2070 (RCP 2.6)	681.98	349.29	129.08	−220.21
Currently–2070 (RCP 8.5)	686.76	344.60	149.43	−195.17

† Number of spatially defined cells under different scenarios at a resolution of 2.5 arc-min × 2.5 arc-min. The expansion minus the contraction was compared with the current distribution.

Table 2. Predicted suitable habitat area changes of *Ostrinia nubilalis* (ECB) from the current and future climatic scenarios

	ECB			
	Area change (100 $^{-2}$ km^{2})			
Climate scenarios	No change	Contraction	Expansion	Total
Currently–2050 (RCP 2.6)	792.62	146.26	94.58	−51.68
Currently–2050 (RCP 8.5)	803.17	135.71	107.33	−28.38
Currently–2070 (RCP 2.6)	813.35	125.53	136.46	10.93
Currently–2070 (RCP 8.5)	819.92	118.96	112.21	−6.75

† Number of spatially defined cells under different scenarios at a resolution of 2.5 arc-min × 2.5 arc-min. The expansion minus the contraction was compared with the current distribution.

ences in the degree of niche shift during their invasion.[55] Recent niche studies have clarified that Zyginelline leafhoppers adapt to the high latitude river-mountain system through the niche shifts.[56] In addition, similar results were found in a study of *Hyphantria cunea* by Tang *et al*. (2021); their results showed that *H. cunea* has adapted to several climatic conditions in China, which indicates the niche of *H. cunea* may shift and as the populations adapt to novel environmental conditions over the course of their spread.[57] The results of this study provide a comprehensive analysis of suitable areas for two corn borers around the world. Our findings indicate clear predicted niche shifts for ACB and ECB in their respective survival areas during the colonization. Furthermore, forecasts for the future show that currently suitable areas would remain stable, particularly in areas where the ACB and ECB are already colonized. In addition, the regions in northeastern Eurasia and middle North America may be highly suitable to be inhabited by ECB.

We found that the survival ranges and niche shifts of both pests were significantly influenced by temperature and precipitation (Fig. 7(a), (b)). This is likely because limiting environmental factors of temperature and precipitation significantly impact the distribution of relevant host plants and cultivation system.[58] The two species do not, however, appear to be influenced by temperature and precipitation equally. Potentially due to differences in their geographical distribution patterns, the ACB (bio4, bio7, bio11 and bio13) was mainly affected by temperature, whereas the ECB (bio12, bio6 and bio17) was more susceptible to precipitation (Supporting Information, Table S1). In this study, ACB is mainly distributed from Sub-frigid zone (50 °N to 65 °N, mean temperature in January is lower than −20 °C) to Subtropics (10 °S to 40 °S, mean temperature in January is higher than 15 °C).[59] Therefore, the ACB populations likely have an abundance of ecological phenotypes to adapt to complex climatic zones. For ECB, during the colonization to new habitat from Eurasia to North America, its survival ranges remained in the climatic zones (40 °N to 60 °N).[72] However, in contrast to the Temperate Marine Climate of native range (Eurasia), the lower precipitation of invasive ranges (North America) might be a limiting factor affecting the life-history traits.[19] These findings imply that bioclimatic variables reflect various characteristics of annual trends, seasonal patterns, and extreme climate, and are related to the eco-physiological suitability of insect species.[60,61]

In this study, limited niche overlaps were observed between native and introduced ranges for both ACB (China and Australia) and ECB (Eurasia and North America) (Table 3 and Supporting Information, Fig. S3). Our niche shift results indicate that the two species experienced various degrees of niche expansion during the colonization of new geographic regions (Fig. 7(c), (d)). The predicted niche expansion could be facilitated by plasticity, evolutionary processes, climate change and by anthropogenic influences (i. e., crop domestication and farm expansion).[62] Analysis of habitat suitability to paleoclimates show habitat suitability prediction results show that the partial habitats of ACB and ECB both decreased from the last interglacial (LIG: 120–140 kya) to last glacial maximum (LGM: 11–29 kya). By contrast, from the LGM to the mid-Holocene, the large-scale expansion of highly and extremely suitability habitats was observed (Figs 5(a) and 6(a)), which could fit the 'glacial refugia'[63] and 'mountain isolation' hypotheses.[64] Similar findings have been obtained for some relative species with fossil records distributed in mountain

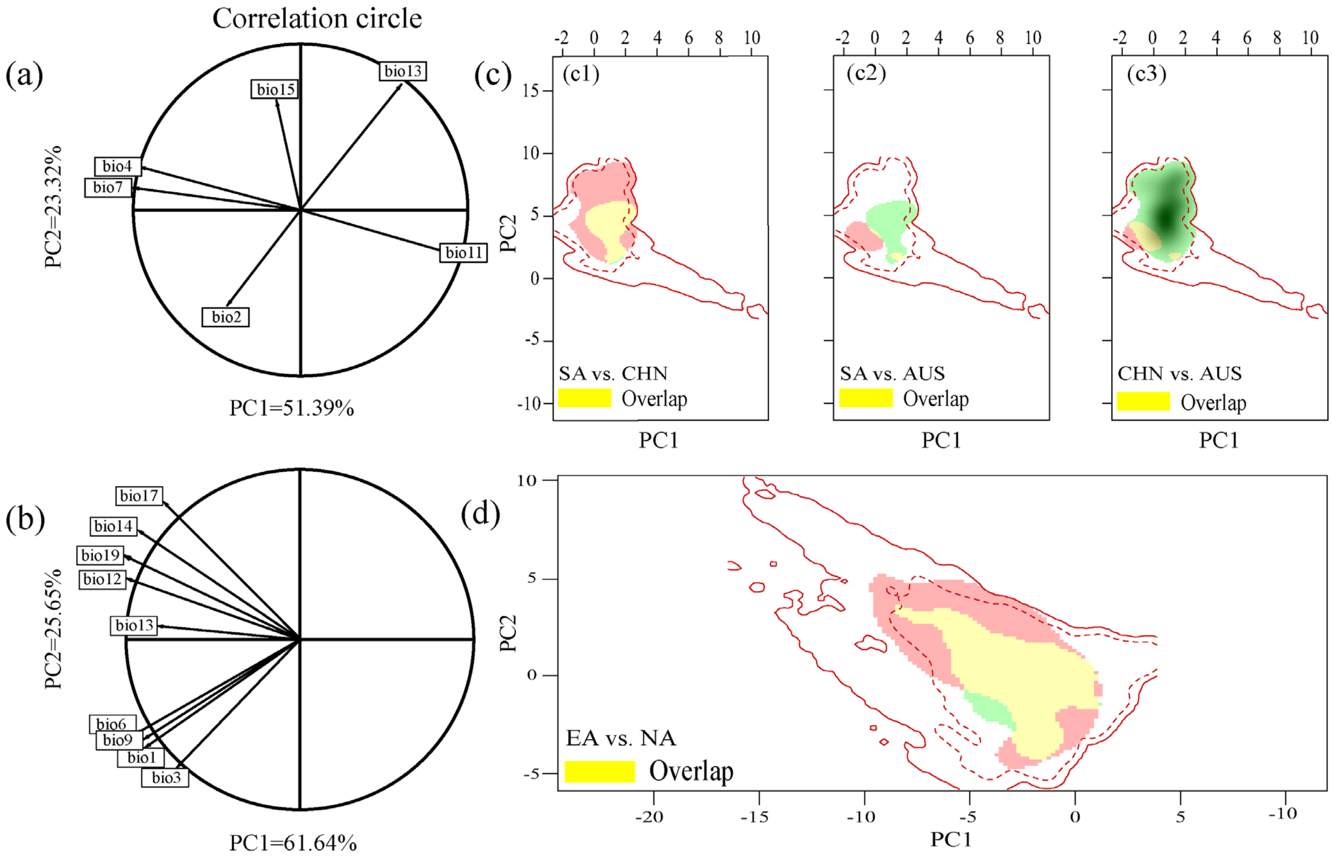

Figure 7. Correlation circle (a) and (b) indicate the single variables used and their contribution towards the two axes (PC1 and PC2) for *Ostrinia furnacalis* (ACB) and *Ostrinia nubilalis* (ECB), respectively, and principal component analysis of niche shift (c) and (d) represent niche overlap for ACB and ECB, respectively. The solid and dashed contour lines illustrate 100% and 50% of the available environmental space, respectively. The niche overlap is visible in yellow and represents stability, the area of unfilling is shown in green, and the zone of expansion is shown in red. Respective region abbreviations for ACB and ECB: Southeast Asia (SA), Australia (AUS), China (CHN), Eurasia (EA), North America (NA).

Table 3. The values of niche overlap between the different geographical populations of *Ostrinia furnacalis* (ACB) and *Ostrinia nubilalis* (ECB) around the world

	ACB					ECB	
	Schoener's *D*		Warren's *I*			Schoener's *D*	Warren's *I*
Distribution areas	CHN	AUS	CHN	AUS	Distribution areas	NA	NA
SA	0.2499	0.0137	0.4890	0.0221	EA	0.1980	0.3723
CHN		0.0074		0.0290	NA		
AUS							

† Respective region abbreviations for ACB and ECB: Southeast Asia (SA), Australia (AUS), China (CHN), Eurasia (EA), North America (NA).

regions.[65–68] These hypotheses assume that the remaining suitability habitat areas gradually grew due to ecological adaptation and/or natural selection after the glacial period.[69]

Previous studies suggested that ACB and ECB have evolved similar phenotypes, ecological niches, and host plant use (maize) based on genetic evidence.[12,17,27] Our habitat suitability prediction results indicate that both ACB and ECB show great niche shift potential and strong adaptability with new habitat colonization, which may have promoted the mismatch distribution and formation of new niche patterns between ACB and ECB.[16,70,71] In addition, our predicted results show that survival ranges of both species will still be greatly concentrated in their initial distributional ranges in the future. Thus, further combined studies on niche shift and genetic architecture of ecological adaptation of ACB and ECB are needed to facilitate in understanding the underlying mechanisms of parallel evolution and speciation in *Ostrinia spp*.

In terms of future expansion predictions, our results show that overall suitable habitat areas of the two species will gradually contract by the 2070s (RCP 2.6) compared with the present (shown in Tables 1 and 2). However, we also found that different types of suitable habitat showed inconsistent trends of area change

(Tables S3 and 4). For ACB, some countries in Eurasia and Oceania such as China, Japan, Korean peninsula and Southeast Asian will expand to encompass areas that are highly suitable for ACB (Fig. 5(b)). For ECB, some specific regions in North America such as the United States and Canada should also be concerned with potential future expansion due to the large corn growing areas that are highly suitable for colonization (Fig. 6(b)). For example, ECB with various habitat suitability co-occur in the main corn production areas of the northeastern USA and Canada.[72] These findings might be meaningful for explorations of ecological traits exclusive to the invasive populations and for eradication measures.

However, there are multiple sources of uncertainty in the present study that could be a focus for future investigations. For instance, comprehensive field investigations have not been carried out throughout Southeast Asia, leading to fewer occurrence records and incomplete estimates of potential habitat. Moreover, host information was not used in this study due to the ambiguous host plants and incomplete host records regarding bioclimatic variables selection. Finally, a limited set of emission scenarios were used (RCP 2.6 and RCP 8.5) in this study, which may result in potential inconsistency of model predictions under different scenarios (such as SSP 126 and SSP 585).[73] Despite these limitations, our findings highlight geographic areas of concern for both pest species, suggesting that improved monitoring and early warning measures are needed in these regions and the surrounding areas.

5 CONCLUSION

In summary, our results showed that temperature and precipitation are significant bioclimatic variables impacting on the niche shifts and potential habitat distribution of two widespread pest species. With the climate change, both ACB and ECB have apparently experienced various degrees of niche shift since they colonized into the new habitats. Particularly, with a large share of native niches remaining unfilled in North American regions, this indicates that ECB has potential for further expanded colonization. Under the future climate scenarios, the ACB's cores of habitat distribution accumulated around eastern coastal areas, and shifted from the corn-growing regions to lower latitudes in China. In addition, the ECB's initial habitat distribution shifted to central-western corn belts in North America. The concentration of their suitable habitats poses a potential threat to future agricultural production. We encourage the application of monitoring and eradication plans whenever possible to prevent naturalization and to avoid further expansion.

AUTHOR CONTRIBUTIONS

BL, EBD and ZFY conceived the ideas and designed the study; BL collected the data; BL analyzed the data; BL and ZFY led the writing of the manuscript. BL, EBD, YLD and ZFY revised the manuscript and contributed to the interpretation and analysis of the data. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank John Richard Schrock (Emporia State University, Emporia, KS, USA) for reviewing the manuscript and greatly improving early versions. In addition, we really appreciate the reviewers for constructive suggestions. This study was supported by the Natural Science Foundation of Shaanxi Province (2023-JC-YB-201), Key Research and Development Program of Shaanxi Province (2023-YBSF-125), China Environmental Protection Foundation (CEPFQS202169-15) and for EBD, Tufts University.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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