

Assessing the current and future biological control potential of *Trichogramma ostrinae* on its hosts *Ostrinia furnacalis* and *Ostrinia nubilalis*

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Abstract

BACKGROUND: Understanding interactions between biocontrol agents and their pest hosts under climate change should assist implementation of biocontrol strategies, by identifying appropriate biocontrol agents for release or determining the optimal timing of releases. Species distribution models (SDMs) were applied to evaluate the distributions of *Trichogramma ostrinae* and its native host, *Ostrinia furnacalis*, in southeastern Asia, and a non-native host, *Ostrinia nubilalis*, in a novel range, North America, using MAXENT and CLIMEX modelling approaches.

RESULTS: The models led to similar predictions about the expected distribution of the two species in Asia, and emphasized likely mismatches between host and natural enemy. *Trichogramma ostrinae* was predicted to occur in the summer corn region of China, with distribution limits linked to its sensitivity to cold, seasonality of radiation and precipitation. The modelled *Ostrinia nubilalis* distribution overlapped with the main corn production areas of the northeastern USA and Canada; temporary/seasonal suitable habitat was also predicted across the southeastern USA. Climate change scenarios are predicted to favour *T. ostrinae* over its hosts in northeastern China and North America.

CONCLUSION: The modelling approaches used here proved useful for assessing environmental factors linked to an egg parasitoid and its lepidopteran hosts and identifying areas potentially suitable for inundative releases.

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

Keywords: biocontrol; CLIMEX; species distribution model; egg parasitoids; environmental niche model; MAXENT

1 INTRODUCTION

Weather extremes driven by climate change are set to challenge crop production, with the potential to destabilize agricultural ecosystems and threaten local to global food security.¹ To maintain sustainable pest control in crop production systems, an understanding of the extent to which climate change will affect both pests and their natural enemies (including predators and parasitoids) is needed. Climate change is expected to drive population asynchrony or coextinction of hosts, parasites and mutualists,² highlighting that increased research attention should be focused on these important ecological relationships. There is a range of approaches for examining effects of climate change on these interactions,³ particularly for changes in the distributions and abundances of host and parasitoid.⁴

To make predictions of species distributions, different types of niche models are increasingly used both in biodiversity conservation and in applied ecology.^{5–7} The choice of which type of model to use is typically determined by the type of data that is available for the species.⁸ A popular form of model is an environmental niche model (ENM) such as Maximum Entropy Modeling (MAXENT), which aims to approximate the realized niche of

species by characterizing species–environment relationships using species occurrence data and environmental covariates. The realized niche inherently includes not only abiotic constraints but also other implicit factors, such as biotic interactions including competition and host availability, as well as the ability of species to disperse through the environment.⁷ Correlative models are thus useful for inferring species–environment relationships and examining the response of the species across its range to specific predictors to better understand distribution limits.^{9,10} While ENMs provide important tools to infer species–environment relationships and limits to distributions, there are issues of transferability

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when extrapolating these models in time and space. Species distributions have also commonly been analysed with CLIMEX, a semi-mechanistic niche modelling tool, adopting a combination of life history parameters with abundance and distribution records. It is broadly used to investigate the interactions between biological invasions, potential response to climate change and efficiencies under climate change scenarios.^{4,10,11} By constructing niche models grounded on species ecophysiological traits, CLIMEX avoids some issues of extrapolation or transferability across regions and future climate change scenarios.¹⁰ CLIMEX determines an ecoclimatic index reflecting the suitability of a location through a combination of growth and stress parameters.¹²

One area where CLIMEX models are useful is for predicting the distribution of classical biocontrol agents. CLIMEX has been used to identify American regions most climatically similar to native localities (southern Africa) of biocontrol agents, and thus efficiently narrowed the search range for natural enemies of two alien pest plants of significant invasion concern worldwide, *Chromolaena odorata* and *Acacia nilotica* spp.^{13,14} Further analyses of this nature should provide valuable information for classical biocontrol strategies, by identifying regions where natural enemies may become mismatched with their hosts, and by identifying periods of time when inundative releases with parasitoids and predators are likely to be effective.¹⁵

An important group of natural enemies are the *Trichogramma* (Hymenoptera: Trichogrammatidae) wasps, small egg parasitoids that help control a range of lepidopteran pests. *Trichogramma* spp. are often cultured and released in inundative biocontrol programmes to successfully aid agricultural production.¹⁶ In comparison to other insect guilds, parasitoids are more likely to be sensitive to climate change¹⁷ and other environmental disturbances because of their position in the trophic web, and because of host specialization (e.g. host generalists responded faster with larger expansion/host shift ranges within habitats).^{18,19} Thus, parasitoids will be affected not only by the direct effects of climate change, but also by indirect effects mediated through changes in host population dynamics.^{17,20}

The Asian corn borer (ACB), *Ostrinia furnacalis* Guenée (1854), is a serious pest of corn and causes more than 9 million tons of yield loss per year.²¹ The geographical range of ACB extends from eastern and southeastern Asia, through to the western Pacific islands.²² The endemic egg parasitoid, *Trichogramma ostriniae* Pang & Chen (1974), is the predominant species parasitizing ACB across the native range, which consists of most of the corn-cropping regions of southeastern Asia.^{21,23} In China, *Trichogramma* biocontrol of ACB has been conducted since the early 1950s; today nearly four million hectares of cornfields are treated with *T. ostriniae* and other *Trichogramma* species across southeastern Asia annually.²¹ Surveys of both *T. ostriniae* and ACB in the native range provide an opportunity to model the current distribution and investigate potential distributions of the host and this parasitoid under climate change scenarios across southeastern Asia.

Because of its success in controlling ACB in China, *T. ostriniae* has been introduced to control the closely related European corn borer (ECB), *Ostrinia nubilalis* (Hübner 1917), in northeastern USA (New York, Massachusetts, Delaware and other locations) and Canada (southern Quebec) since the early 1990s.^{24–26} The ECB is endemic to Europe and western Asia and was introduced to northwestern America in the early 19th Century. Early inoculative releases of *T. ostriniae* showed promising results, with up to 80% of parasitism achieved in cornfields in this region.²⁷ Inoculative releases are currently available as an option to help control European corn borer in

sweet corn in New York, Kentucky and other states in northeastern USA.²⁸ Given the status of these important lepidopteran pests and the active *Trichogramma* biocontrol programmes in place, these data provide a unique opportunity to test projections of niche models within and between continents, and assess the future effectiveness of biocontrol under climate change scenarios.

In this current study, we employed niche modelling to determine climatic factors associated with two lepidopteran host species and the biocontrol parasitoid, and examine potential changes in their distributions as a consequence of climate change. The specific aims of the current study were: (1) to analyse and compare species–environment relationships and niche overlap of *T. ostriniae* and its host moth ACB across their native distribution in Asia; (2) to better understand the suitability of the climate for *T. ostriniae* in North America for control of ECB; and (3) to examine how host–parasitoid relationships of ACB in Asia and ECB in North America may be altered under climate change. Determining how broad-scale climate patterns may change host–parasitoid relationships should help in planning future biological control programmes.

2 MATERIALS AND METHODS

As we had data from different knowledge domains, including field observations of distribution and phenology, physiological response information, and models of diapause, we constructed different models where appropriate.

2.1 Distribution data

Occurrence data were obtained from published references (see Supporting Information Appendix S1) [$n = 111$ for *T. ostriniae*; $n = 149$ for *O. furnacalis* (ACB)], field surveys around southwestern Taiwan in 2014 and 2015 ($n = 9$ for *T. ostriniae*; $n = 28$ for ACB; Wu et al.²³ and CH Hsieh, pers. comm.) and the Global Biodiversity Information Facility (GBIF) database [$n = 404$ unique points for *O. nubilalis* (ECB)] (Fig. 1). *Trichogramma ostriniae* is not currently used in Europe as a biological control agent for ECB. The North American distribution of *T. ostriniae* listed (Table S1) was not used in model training (see below) as these data were obtained from successful inundative releases in biological control programmes, and it is not clear if permanent populations have established at these release points.²⁹ Instead, these points were used to test whether the predictions from the models matched those where inundative releases have taken place.²⁹

2.2 Environmental data

We obtained environmental data from CliMond,³⁰ which provides data formats suitable for both correlative ENMs and CLIMEX models. For ENM model construction, CliMond provides 35 bioclimatic variables describing means, seasonality and trends for temperature, precipitation, solar radiation and soil moisture. Data for CLIMEX use the same observations, but use daily minimum and maximum temperatures, monthly precipitation and relative humidity. We used a grid cell resolution of 10' for both approaches, which is approximately 20 x 20 km at the Equator.

2.3 ENM construction

For the construction of correlative distribution models for *T. ostriniae* and its host *O. furnacalis* (Fig. 2), we ran MAXENT (version 3.3.3i)³¹ which uses the principle of maximum entropy to relate distribution records of a species to environmental variables for

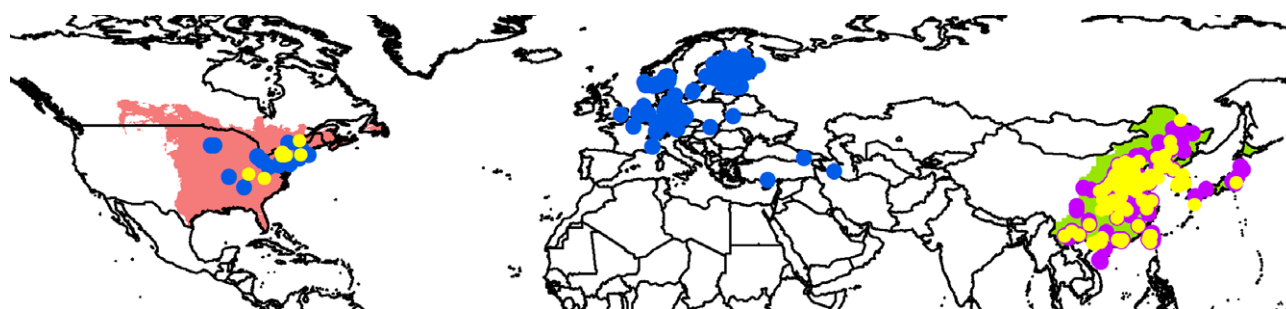


Figure 1. Distributions of Asian corn borer, *Ostrinia furnacalis* (purple circles), European corn borer, *Ostrinia nubilalis* (blue circles), and *Trichogramma ostrinae* (yellow circles). Sources are published references (see Table S1) and field surveys in 2014 and 2015 in China, Japan, Korea and Taiwan. Locations of *T. ostrinae* inundative releases undertaken in North America are from published references (see Appendix S1). Coloured areas represent backgrounds used in environmental niche model (ENM) construction based on Köppen–Geiger classifications (green, Asia model; pink, America model).

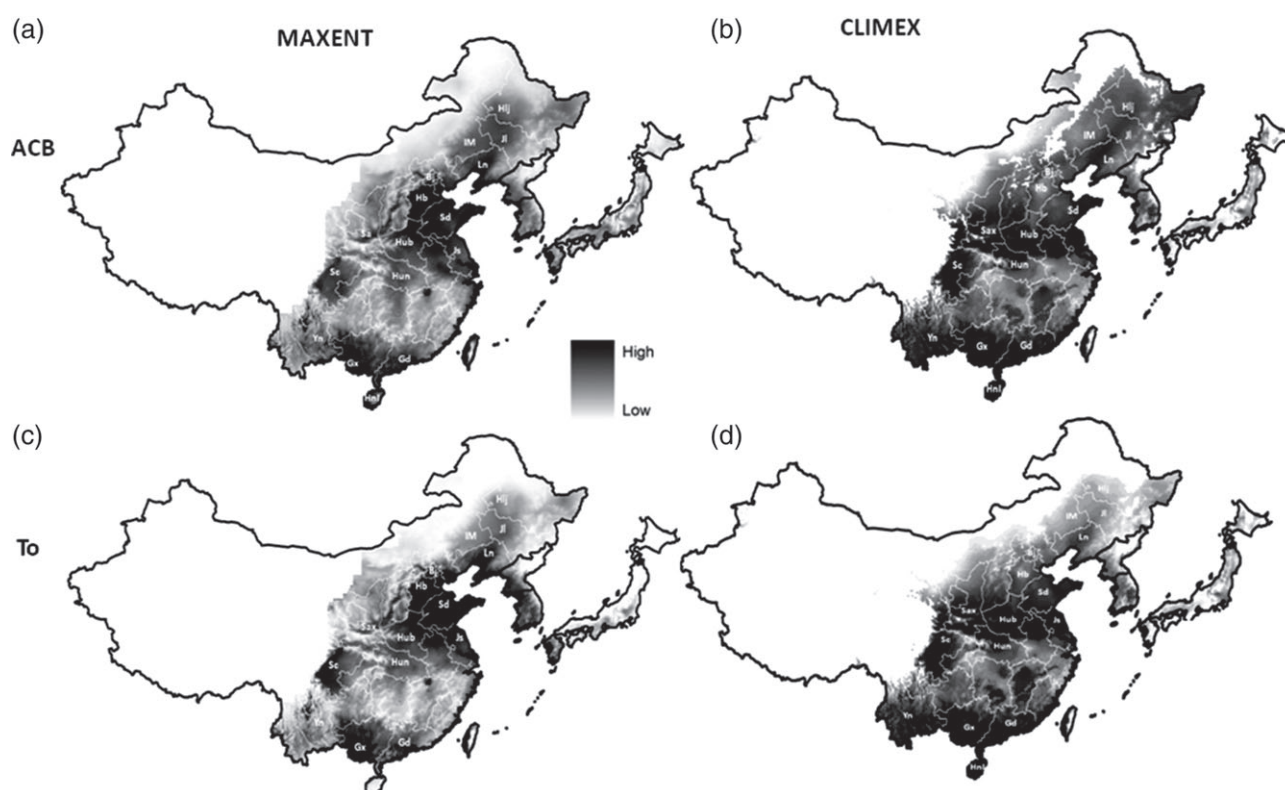


Figure 2. Distribution fitting models between *Ostrinia furnacalis* (ACB) and *Trichogramma ostrinae* (To) in southeastern Asia using two different niche modelling approaches. (a) *Ostrinia furnacalis* logistic MAXENT fitting model: MAXENT logistic output is shown as a continuous suitability (0–1) layer, and darker shading indicates higher climate space suitability. (b) *Trichogramma ostrinae* logistic MAXENT fitting model. (c) *Ostrinia furnacalis* and (d) *T. ostrinae* CLIMEX fitting model: El output is shown as a continuous suitability (0–65) layer, and darker shading indicates higher climate space suitability. Provinces are indicated on the map by abbreviations: Ah, Anhui; Bj, Beijing; Fj, Fujian; Gd, Guangdong; Gs, Gansu; Gx, Guangxi; Gz, Guizhou; Hb, Hebei; Hlj, Heilongjiang; Hn, Henan; Hnl, Hainan Island; Hub, Hubei; Hun, Hunan; IM, Inner Mongolia; Jl, Jilin; Js, Jiangsu; Jx, Jiangxi; Ln, Liaoning; Sax, Shaanxi; Sc, Sichuan; Sd, Shandong; Sx, Shanxi; Yn, Yunnan; Zj, Zhejiang.

estimating the potential distribution of the targeted organism.^{31,32} MAXENT uses information on conditions in the region of interest as a basis for comparison with conditions at known presence sites, so the regions ('background') need to be defined before model construction. We first set the background for the native range to occupied bioclimatic regions from Köppen–Geiger classifications within (or intersecting) the borders of China, Japan, North Korea, South Korea and Taiwan, because all our data points were contributed by publications from these areas (Fig. 1). Köppen–Geiger classifications followed the rules defined in Kriticos *et al.*³⁰ as applied to the 10' resolution CliMond global climatology [sourced from the WORLDCLIM and Climate Research Unit (CRU) datasets;

<http://worldclim.org>; version 1.4, release 3³³; <https://crudata.uea.ac.uk/cru/data/hrg/>; version CL2.0³⁴]. This provides a broad geographical area to account for data availability and occurrence record biases, but omits large geographical areas that are not relevant to modelling species distributions.³⁵

To determine key variables for model inclusion, we applied environmental niche factor analysis (ENFA)³⁶ for the two species datasets independently across their respective backgrounds using the 'adehabitat' package³⁷ in R (version 3.1.1).³⁸ Variables were ranked on marginality, which describes the difference between the total range of environmental variables and the range occupied by the species, within the accessible area.³⁶ The top 10 variables

for both species were then checked for spatial autocorrelation. We generated 10 000 random points across each background, extracted variable information for each of the environmental predictors, and conducted pairwise Pearson correlation tests across all variables. For variables that were highly correlated ($r > 0.75$), a variable from the pair was removed based on a lower marginality score.³⁹ By removing variables in this manner, we could reduce issues that may be caused by multicollinearity, and its bias on models projected to novel regions.⁴⁰ To enforce smooth response curves, we only enabled hinge features (see Elith *et al.*⁹; Hill & Terblanche⁴¹); all other parameters were left at default. Models were then run using 10 cross-validation replicates, taking the average of all replicates for spatial predictions. The respective predictor variable sets were then examined using the jackknife feature of MAXENT together with percentage contribution to the model.

To test for any changes to model performance from possible sampling error, we also created a buffer zone of 20 km around each location assigned using literature records and randomly jittered locations (see Hill *et al.*⁴²). The resulting mapped predictions were compared through niche overlap analysis (Schoener's *D* statistics) using the 'dismo' package⁴³ in R. We then performed a one-tailed *t*-test to determine whether the actual dataset produced models different from those with random error incorporated (Appendix S1).

2.4 Environmental space

In addition to modelling the distributions of all species, we examined overlap in multivariate environmental conditions across the different geographical regions. We extracted predictor information for a common predictor variable set that included all important variables across the distribution of all species. We then sampled 10 000 random points across the Asia and North America backgrounds and extracted the same climatic information at these points. We performed principal components analysis (PCA) for the total combined data, and plotted the first two axes to visually examine overlap between the different species, and the background datasets (Appendix S2).⁴¹

2.5 CLIMEX modelling

The CLIMEX model processes a series of weekly growth and stress indices that are combined to derive an ecoclimatic index (EI). The EI indicates regions that are unsuitable for the species to persist, compared with those that provide an ideal environment for the species. The EI scale ranges from 0 to 100, with 0 representing an unfavourable environment, values > 20 considered to represent ideal conditions, those between 10 and 20 considered to represent suitable conditions, and those between 0.01 and 10 considered to represent marginally suitable conditions,⁴¹ although interpretations of EI are species-specific to some extent.¹⁰ For ACB and *T. ostrinae* CLIMEX models, initial parameter values were provided by a template species, the Colorado beetle, *Leptinotarsa decemlineata* (Say), as it is also an important agricultural pest inhabiting similar latitudes, and its default simulation fitted well with known distributions. For ECB, initial parameter values were acquired from previous modelling attempts⁴⁵ and refined using its native European distribution. To fit the CLIMEX model for each of *T. ostrinae*, *O. furnacalis* and *O. nubilalis*, the species' known native distributions together with reported range descriptions were used to iteratively adjust the model until the CLIMEX simulated geographical distribution coincided with its known distribution.

Both species here undergo facultative diapause as later stage larvae to escape suboptimal cold conditions, especially at higher latitudes. Diapause in CLIMEX is incorporated through a relationship between photoperiod and temperature. The diapause index is an important component in determining the yearly growth index (GI), and can be adjusted according to observations from trap captures and field observations for the species. Below we describe where we made parameter changes, and the rationale for each, for the three species under investigation.

2.6 Parameters for *O. furnacalis* (ACB)

2.6.1 Temperature index

Lower developmental threshold ranges were 6.8 to 10.4 °C for *O. furnacalis*.²² In the current study, the minimum temperature for development (DV0) was set at 6.8 °C. The lower and upper optimum temperatures (DV1 and DV2, respectively) were set at 20 and 28 °C, respectively. The upper temperature threshold was close to 33–35 °C, so the upper threshold temperature (DV3) was set at 33 °C.

2.6.2 Moisture index

Moisture index values limited the establishment of both species in western China and across the southeastern mountain areas. The lower soil moisture limit for development (SM0) was set to 0.15 to indicate the lowest moisture threshold points of the egg parasitoid and its lepidopteran host. This limit normally corresponds to a soil moisture level of approximately 10%. The lower and upper optimal moisture index (SM1, SM2) and upper limit (SM3) were set to levels considered biologically reasonable for current distributions, or 0.35, 0.80 and 1.5, respectively.

2.6.3 Cold stress

For ACB cold stress, temperature threshold (TTCS) and cold stress accumulation rate (THCS) were set to 0.5 °C and $-0.0001 \text{ week}^{-1}$, respectively. EI in northeastern China would be too low if its TTCS parameter had higher values. Furthermore, higher TTCS values would not be consistent with the known distribution of ACB in northeastern China, where it is widespread and causes high damage levels. THCS values were adjusted iteratively to fit the distribution boundaries for ACB.

2.6.4 Heat stress

Heat stress was increased by setting the heat stress temperature threshold (TTHS) to 33 °C and heat stress accumulation (THHS) to 0.002 week^{-1} , to prevent southern parts of Indochina and other tropical areas becoming suitable.

2.6.5 Diapause index

In its subtropical and temperate geographical range, ACB enters a facultative cold diapause in the late larval stage from late summer to early spring.²² Diapause has been studied in different parts of the species range, including China and Japan. In general, declining photoperiod experienced by the larval stage determines the proportion of the population entering cold diapause, with warm temperatures and photoperiod in spring determining the timing of termination.^{22,46} In China, Guo *et al.*⁴⁷ noted that the critical day lengths for diapause induction of ACB among four geographical populations declined from the north towards the south and the sensitivity to photoperiod also declined from north to south in the populations. At the same time, the critical day length would

Table 1. CLIMEX parameter values for the final model for *Ostrinia furnacalis*, *Trichogramma ostrinae* and *Ostrinia nubilalis* determined by iteratively changing parameter values until the performance provided the best fit to the known native distributions (see Fig. 1)

Index	Parameter	Value ^a		
		<i>O. furnacalis</i>	<i>T. ostrinae</i>	<i>O. nubilalis</i>
Temperature (°C)	DV0 = lower threshold	6.8	11.7	5.5
	DV1 = lower optimum temperature	20	22	28
	DV2 = upper optimum temperature	28	29	38
	DV3 = upper threshold	33	35	41
Moisture	SM0 = lower soil moisture threshold	0.15	0.15	0.06
	SM1 = lower optimum soil moisture	0.35	0.35	0.15
	SM2 = upper optimum soil moisture	0.80	0.80	1.20
	SM3 = upper soil moisture threshold	1.50	1.50	2.00
Cold stress	TTCS = cold stress temperature threshold (°C)	0.5	1	-
	THCS = cold stress accumulation rate (week ⁻¹)	-0.0001	-0.0001	-
Heat stress	TTHS = heat stress temperature threshold (°C)	33	35	30.5
	THHS = heat stress accumulation rate (week ⁻¹)	0.002	0.02	0.01
Dry stress	SMDS = dry stress threshold	0.1	0.1	0.05
	HDS = dry stress rate (week ⁻¹)	-0.02	-0.02	-0.04
Wet stress	SMWS = wet stress threshold	1.5	1.5	1.5
	HWS = wet stress rate (week ⁻¹)	0.0002	0.0002	0.0002
Diapause	Diapause induction daylength (h)	14.88	-	14.5
	Diapause induction temperature (°C)	17	-	12
	Diapause termination temperature (°C)	6	-	10

^a Values without units are dimensionless proportions. Cold stress parameters for *O. nubilalis* are left blank as these would not affect the model outcome.

be shortened when the rearing temperature increased from 20 to 27 °C. We set the diapause induction daylength to 14.88 h, the induction temperature to 17 °C and the termination temperature to 6 °C. These values were obtained from Lu and Zhou⁴⁸ and then the growth index was iteratively fitted around population observations from Yang *et al.*⁴⁶

2.7 Modelling for *O. nubilalis* (ECB) in Europe and North America

2.7.1 Temperature index

The mean lower developmental threshold was 10 °C in previous modelling attempts.^{45,49} In the current study, the minimum temperature for development (DV0) was set at 5.5 °C to capture the northern distribution points in Scandinavia better; the lower and upper optimum temperatures (DV1 and DV2, respectively) were set at 28 and 38 °C, respectively; in line with parameter estimation from Maiorano *et al.*⁴⁹, we set the upper limit to 41 °C.

2.7.2 Moisture index

Moisture index values limited the establishment of *O. nubilalis* in central USA and across the mountain areas. The lower soil moisture limit for development (SM0) was set to 0.06 to indicate the lowest moisture threshold points. The lower and upper limits for optimal growth (SM1, SM2 and SM3) were set to levels considered biologically reasonable for current distributions, which were 0.15, 1.2 and 2, respectively.

2.7.3 Cold, dry and heat stress

As the temperature index for *O. nubilalis* alone was able to define the northern (colder) range, adjustments of cold stress parameters were not expected to affect the model outcome and were omitted. Dry stress relates to the moisture index, and the dry stress

threshold (SMDS) was set to 0.05 and the dry stress rate (HDS) to -0.04 week⁻¹. Heat stress was lowered, by increasing the heat stress temperature (TTHS) to 30.5 °C and heat stress accumulation (THHS) to 0.01 week⁻¹ to prevent southern parts of the USA and Mexico becoming suitable. Parameters used in CLIMEX models are listed in Table 1.

2.7.4 Diapause index

The diapause induction day length and temperature were set at 14.5 h and 12 °C, respectively, in previous modelling attempts.^{45,49} In the current study, the diapause termination temperature was lowered to 10 °C, better capturing the emergence time of ECB adults for Pontevedra in northwestern Spain.⁵⁰

The CLIMEX model for ECB was compared to previous model results from Trnka *et al.*⁵¹ and Svobodová *et al.*⁵². Because CLIMEX also models the weekly suitability of climate for population growth, it is possible to verify phenology as well as different geographical establishments.³⁰ The modelled weekly growth index phenology (GI_w) was compared to field moth capture numbers from two locations in Spain (Pontevedra and Barrantes) for *O. nubilalis* validation in Europe.⁵⁰ For North America, we tested our model performance with published data points.^{26,53,54}

2.8 Parameters for *T. ostrinae*

2.8.1 Temperature index

Lower developmental thresholds were around 11.7 to 11.8 °C for *T. ostrinae*.⁵⁵ In the current study, the minimum temperature for development (DV0) was set at 11.7 °C. The lower and upper optimum temperatures (DV1 and DV2) were set at 22 and 29 °C, respectively.²⁹ The upper temperature threshold for both species

was close to 33–35 °C, so the upper threshold temperature (DV3) was set at 35 °C.

2.8.2 Cold stress

For *T. ostriniae*, the cold stress temperature threshold (TTCS) and cold stress accumulation rate (THCS) were set to 1 °C and -0.0001 week⁻¹, respectively. THCS values thus were adjusted iteratively to fit the distribution boundaries for *T. ostriniae*.

2.9 Host–parasitoid dynamics under climate change in Asia and North America

To explore possible host–parasitoid dynamics in distribution under climate change for ACB and *T. ostriniae* in Asia, and for ECB and *T. ostriniae* in North America, we used the CSIRO Mk. 3.0 models (available from CliMond)³⁰ for the year 2080 under the A1B Special Report on Emissions Scenarios (SRES) for future climate change, one of the higher rates of warming in the Fourth Assessment Report (AR4).⁵⁶ We further investigated the impact of the predicted changes by plotting the difference in the GI for both corn borers (ACB/ECB) and the GI for *T. ostriniae* as a proportion of the GI for ACB/ECB in Asia and North America, and presented proportions as a measure of the likely effectiveness of *T. ostriniae* as an inundative biological control agent on these two continents.

3 RESULTS

3.1 Distribution fit and model projections for *O. furnacalis* and *T. ostriniae* in Asia

The predicted native range of ACB overlaps with the main corn production areas that are within northeastern (Heilongjiang, Jilin and Shenyang Provinces), eastern (Beijing, Hebei, Henan, Shandong, Shanxi, Jiangsu and Anhui Provinces), and southeastern (Guangdong, Guangxi and Yunnan including Hainan Provinces) China, Japan and southwestern coastal regions of Taiwan (Figs 2a,c). The predicted range of *T. ostriniae* (Figs 2b,d) is similar to that of its host *O. furnacalis*, except for its more constrained northern limits in China and Japan, and there are no presence data for Hainan Island.

Variable importance was similar and a final suite of five variables was common to both species after our selection procedure (Table 2). MAXENT performed well in terms of the area under the curve (AUC) scores, estimated on held-out cross-validation data within the training areas (Table 2). Varying locations up to 20 km did not significantly change model predictions (Appendix S1). The mean temperature of the wettest quarter (°C) (bio08) was the most influential variable for the two species; precipitation and radiation seasonality (bio15 and bio23, respectively) were also important, each contributing >10% (Table 2). CLIMEX predicted suitable areas for *O. furnacalis* in Jiangsu and Yunnan (Figs 2a,2c), whereas MAXENT predicted the constrained distribution of *T. ostriniae* well in Jiangsu, Gansu, Shaanxi and Hainan Provinces, although its performance tended to be over-conservative in Yunnan Province (Figs 2b,d).

Figure 3 shows the response curves for the variables used in our MAXENT models. Each curve represents the response to a specific variable with all others set constant, and should therefore be interpreted cautiously, although comparisons between species and models do allow for testable biogeographical insights.⁴² The responses indicate that the distributions of both species are correlated with the mean temperature of the wettest quarter in summer rainfall corn production regions (bio08) in the range 10–29 °C (Fig. 3), with both species preferring areas with higher

summer precipitation and precipitation seasonality (bio18 and bio15) within areas that possess moderate isothermality (bio03). Overall, the shapes of response curves were similar between ACB and *T. ostriniae*, although the starting points for precipitation and radiation seasonality were higher for ACB. The response curve displayed an opposite trend to radiation seasonality in ACB. This difference suggests that *T. ostriniae* is more sensitive to climatic seasonality. Permutation importance of precipitation and radiation seasonality in both species models was 18.13 and 23.33, respectively, for *T. ostriniae*, compared with 14.08 and 10.03, respectively, for ACB (Table 2).

3.2 Distribution fit and model projections for *O. nubilalis* and *T. ostriniae* in Europe and North America

The locations for inundative release of *T. ostriniae* are in central and northeastern USA and Canada (Kentucky, Virginia, Massachusetts and New York States and Quebec; Fig. 1). Each of the final variable sets used in the MAXENT, PCA analysis and Multivariate environmental similarity surface (MESS) map for North American projections (see Appendix S2 for details) indicated that accessible climate space available to *T. ostriniae* distributed in native Asia is not accessible in novel North America regions. Dissimilar climate space between those two continents might have constrained the MAXENT projection for *T. ostriniae*; thus, only the CLIMEX model was adopted for model projection across continents.

The modelled native distribution of *O. nubilalis* covers the whole of Europe, including England and the southern margin of the Scandinavian peninsula (Fig. 4). The distribution is consistent with model results from Trnka *et al.*⁵¹ and Svobodová *et al.*⁵² in the Czech Republic and most European areas, taking into account the use of different climate backgrounds here, and the expected minor idiosyncrasies between datasets. Another test of the CLIMEX model is to generate weekly changes in GI_w over an average year for a location and compare this 'modelled suitability' with observed phenology based on trapping of adult moths (Fig. 4). GI_w would be expected to be an indicator of population growth rate for *O. nubilalis*. For both sites, trapped moths occur at times that are climatically suitable for growth, with a 7-week delay for adults observed in Barrantes (northwestern Spain). Moth numbers will of course reflect additional landscape-level effects of crop availability and 'management', such as extensive and intensive spraying of insecticides.^{57,58}

The modelled distribution of *O. nubilalis* in North America overlaps with the main corn production areas and published distribution points for *O. nubilalis*^{26,53,54} that are within the northeastern USA (Iowa, Illinois, Indiana, Ohio and nearby areas) and Canada (Quebec) (Fig. 5a). Moreover, there is contiguous suitable habitat across southeastern states for the modelled distribution of *T. ostriniae* (Fig. 5b).

3.3 Host–parasitoid dynamics under climate change in Asia and North America

Using the difference in GI between ACB/ECB and *T. ostriniae* allows us to comment on the effectiveness of *T. ostriniae* as a biological control agent under current and future conditions. Current climates in Asia are predicted to favour *T. ostriniae* over ACB across China (Fig. 6a; purple shading), and ACB only has higher GI in the Sichuan area (Fig. 6a; yellow shading). By 2080, it is predicted to favour *T. ostriniae* over ACB in northeastern China as the difference between GI for ACB and GI for *T. ostriniae* increases in these regions. In contrast, the GI of ACB is predicted to decline

Table 2. Sample size and percentage based on mean area under the curve of receiver-operator characteristic (AUC) test gain across 10 cross-validation replicates for MAXENT models; final variable^a contributions and importance were assessed through MAXENT selected for *Trichogramma ostrinia*e and *Ostrinia furnacalis*

Species	n	AUC	Variable contribution and importance									
			Bio03		Bio08		Bio15		Bio18		Bio23	
			PC	PI	PC	PI	PC	PI	PC	PI	PC	PI
<i>O. furnacalis</i>	183	0.778	9.64	8.22	62.11	61.88	12.77	14.08	5.43	5.80	10.06	10.03
<i>T. ostrinia</i> e	129	0.854	5.10	5.27	58.07	52.47	19.29	18.13	1.05	0.80	16.48	23.33

^a Bio03 = isothermality [mean of monthly (maximum temperature – minimum temperature)/temperature annual range] (× 100); Bio08 = mean temperature of wettest quarter (°C); Bio15 = precipitation seasonality (coefficient of variation); Bio18 = precipitation of warmest quarter; Bio23 = radiation seasonality (coefficient of variation). PC, percent contribution; PI, permutation importance.

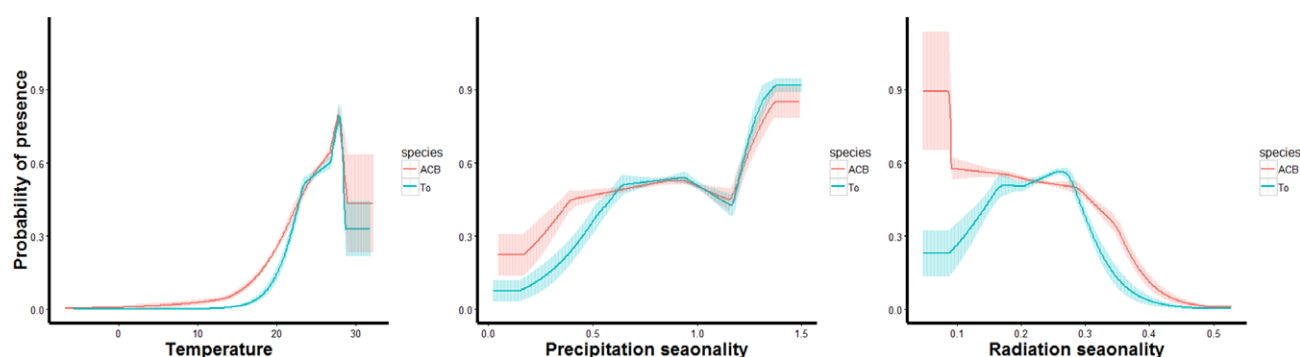


Figure 3. Variable response curves for three dominant predictor variables across models of *Ostrinia furnacalis* and *Trichogramma ostrinia*e built in MAXENT. The line on the graphs is the mean of 10 cross-validation replicates, and the shaded area is the standard deviation across the replicates. Red: *O. furnacalis* (ACB); blue: *T. ostrinia*e (To).

through the Sichuan area (Fig. 6b; previously yellow shading in Fig. 6a changes to light purple shading). The predicted higher temperature by 2080 is likely to favour *T. ostrinia*e in southern China, where the GI for the parasitoid is predicted to be greater than the GI for ACB (Fig. 3c; light purple shading in Fig. 6c changes to dark purple shading).

For North America projections, the climate change scenario is predicted to favour *T. ostrinia*e over ECB around most of the USA and Canada except some southern area (Fig. 6b). By 2080, there is a northward shifting tendency for these areas (Fig. 6d). The predicted higher temperatures by 2080 could favour *T. ostrinia*e from regions in southern Canada (Fig. 6d; dark purple shading) as the difference between GI for ECB and GI for *T. ostrinia*e decreases in these regions. At the same time, higher temperature is predicted to favour ECB in most of the southern USA, where their GI difference is predicted to be amplified (Fig. 6d; light purple shading in Fig. 6c changes to yellow and light-yellow shading).

4 DISCUSSION AND CONCLUSIONS

Understanding the extent to which host–parasitoid relationships may be altered by climate change has important implications for future biological control release programmes. Identifying where putative spatial mismatch between species may occur is particularly important. By employing modelling methods appropriate to the data available on the Asian and European corn borers (ACB and ECB, respectively), and the *Trichogramma* parasitoid (*T. ostrinia*e), we identified broad-scale patterns that provide insights into the importance of precipitation and radiation seasonality which might determine the distribution of a pestiferous host

(ACB) and its parasitoid (*T. ostrinia*e). Our analyses also enabled identification of suitable areas for inundative release of *T. ostrinia*e, which represent areas of likely successful parasitism.

As for most insects, temperature is the key factor that determines the distribution of parasitoids and their hosts across multiple scales.^{17,59} Differences in thermal requirements appear to be responsible for large discrepancies between host and parasitoid distributions. In northern areas of Asia where our models typically predicted more suitable climate space for ACB over *T. ostrinia*e under current conditions, two factors might contribute to this. First, the lower development temperature threshold of *T. ostrinia*e is higher than that of its host (6.8 to 10.4 °C for ACB; 11.7 to 11.8 °C for *T. ostrinia*e).^{22,55} Secondly, ACB demonstrates broader thermal requirements for development than *T. ostrinia*e, which may reflect geographical variation in physiological thermal limits; Xie *et al.*⁶⁰ previously noted variation in the supercooling point (SCP) and survival rate after low-temperature treatments in this species, with mean SCP significantly declining from –22 °C in a tropical population (Haikou, 19.98° N) to –28.5 °C for a univoltine low-temperature population (Gongzhuling, 43.55° N).

For southern areas of Asia, *T. ostrinia*e appears to be more sensitive to the lower seasonality of radiation and precipitation (Fig. 3) than its host. The different responses of *T. ostrinia*e and ACB to seasonality of both precipitation and radiation reflect findings from a meta-analysis for *Trichogramma* parasitism,⁶¹ which found that parasitism was higher in regions with less temperature and precipitation seasonality. *Trichogramma* displays a more restricted climate tolerance than its hosts as the modelling approach is based on occurrence data, and the occurrence and abundance of *Trichogramma* are dependent on the abundance of its hosts.

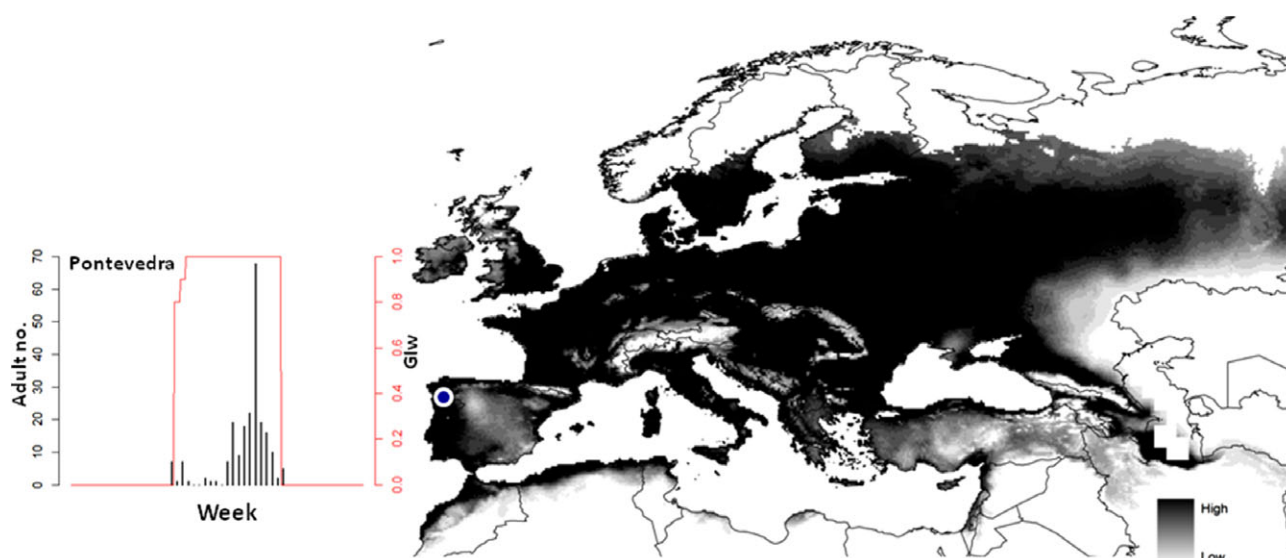


Figure 4. CLIMEX output for European corn borer *Ostrinia nubilalis* in Europe built on CliMond data sets. Shading reflects the ecoclimatic index (EI), and various measures of population abundance for *O. nubilalis* (major y-axis) and weekly growth index (minor y-axis) values over a year derived from current model (time in weeks; 1–52) match with each other in summer for Pontevedra (blue point) in northwestern Spain (modified from Cordero *et al.* 1998).

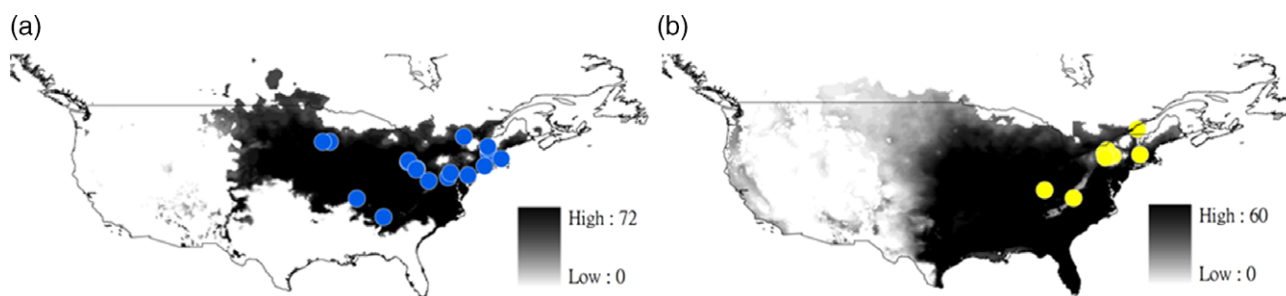


Figure 5. Distribution fitting models between *Ostrinia nubilalis* and *Trichogramma ostriniae* in North America built on CliMond data sets. (a) *Ostrinia nubilalis* and (b) *T. ostriniae* CLIMEX fitting EI model: output is shown as a continuous suitability (0–80) layer, and darker shading indicates higher climate space suitability. Blue points represent distribution points of *O. nubilalis*; yellow points represent distribution points of *T. ostriniae*.

Occurrence data for the hosts are better than for *Trichogramma* parasitoids. At the edge of the geographical range of the hosts, we expect low host population densities and thus low parasitoid densities, making parasitoids particularly hard to detect. As a result, the abiotic tolerance of the parasitoid is estimated as being lower. However, this may also reflect the poor mobility of the parasitoid compared with its host (suggesting that the parasitoid cannot easily track changes in favourable conditions, and, being restricted to the static egg stage of its ACB host, is more exposed to extreme temperature and precipitation), or the dependence of *T. ostriniae* on passive transport (mainly wind dispersion), compared with its larger bodied lepidopteran hosts.^{62,63}

The EIs of *T. ostriniae* and its host ECB in North America were associated with different temperature, moisture, dry and heat stress parameters. In low latitudes of North America, we found that there is more suitable climate space for *T. ostriniae* than ECB (Fig. 5), which is different from predictions in Asia, despite the upper development temperature threshold being higher for the host (41 °C for ECB; 35 °C for *T. ostriniae*).^{49,55} In this case, we suspect that much lower heat stress temperature (30.5 °C for ECB; 35 °C for *T. ostriniae*) and higher heat stress accumulation for ECB (0.01 week⁻¹ for ECB; 0.02 week⁻¹ for *T. ostriniae*) reflect constrained growth and dispersion in southern areas of North America.

Constructing niche models at a global scale inherently assumes that all populations respond to predictor variables, or ecophysiological indices, in much the same way. This is highly unlikely, as differences in temperature-related life history parameters for *T. ostriniae* are likely to exist. For example, individuals from North American populations grow faster than those from Chinese populations (9 days at 24 °C for America; 10 to 11 days at 25 °C for China).²⁹ There may also be genetic differentiation among North America populations of ECB related to voltinism.⁵³ Such differences could influence the successful establishment of *T. ostriniae* populations in new areas. For species that encompass large geographical ranges, it can be challenging to define diapause as a single function for all populations. For ACB and ECB, there are different strains and varying responses to light and temperature according to latitude.^{47,60,64} Whilst we have fitted single diapause indices to these species, it should be noted that regional assessments of distributions and field efficacy will need to identify specific temperature limits and diapause cues for the local populations. Additionally, identifying different populations and strains through genetic methods could allow for partitioning correlative models like MAXENT to investigate species–environment relationships at finer scales.⁶⁵

The underprojection of the *T. ostriniae* Asia-trained MAXENT model onto North America highlights some potential limits

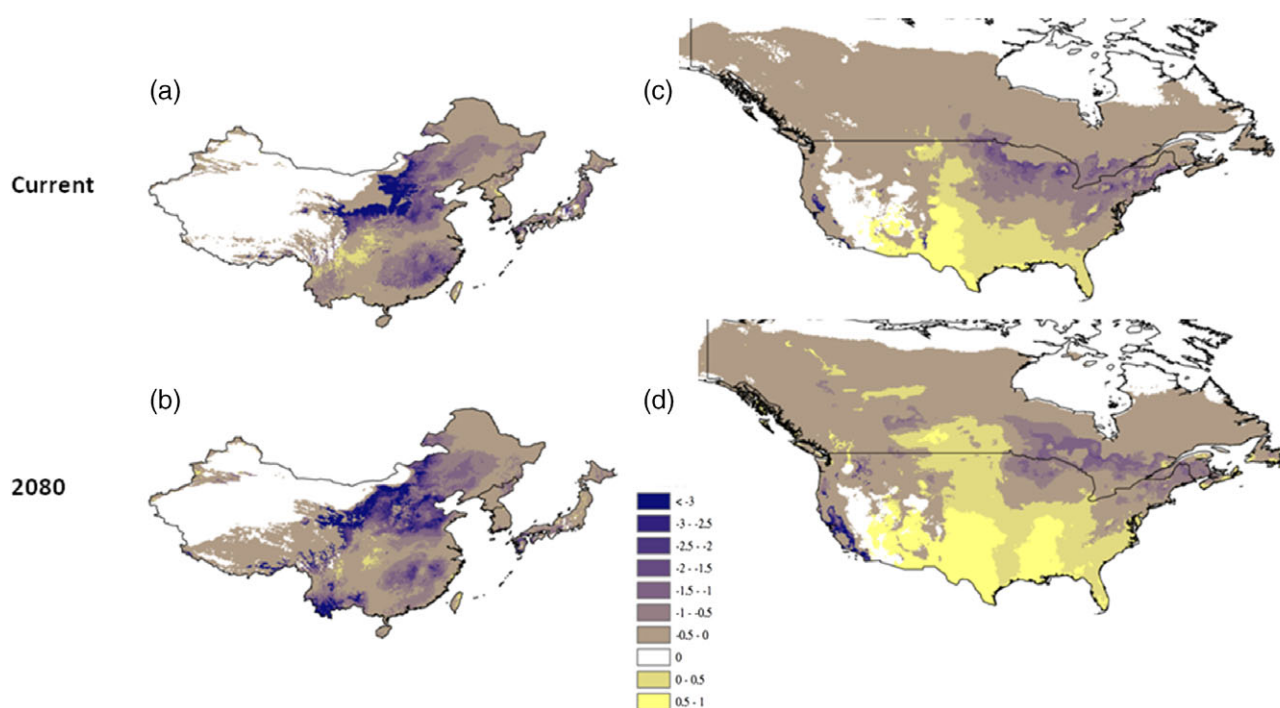


Figure 6. Effects of predicted climate change on the relationships between ACB/ECB and *Trichogramma ostrinae* in southeastern Asia/North America. The relationship between the current differences between ACB, ECB and *T. ostrinae* growth indices (GIs) and the predicted differences in these indices by 2080 is shown. (a) Differences between ACB GI and *T. ostrinae* GI expressed as a proportion of ACB current GI. (b) Predicted differences between ACB GI and *T. ostrinae* GI expressed as a proportion of ACB GI for 2080. (c) Differences between ECB GI and *T. ostrinae* GI expressed as a proportion of ECB current GI. (d) Predicted differences between ECB GI and *T. ostrinae* GI expressed as a proportion of ECB GI for 2080. Dark purple shading shows locations where GI differences for *T. ostrinae* are greatest, and lighter purple shows locations where differences are less pronounced; yellow shading shows locations where ACB/ECB GI is greater than *T. ostrinae* GI and white shading shows locations where ACB/ECB GI is equal to *T. ostrinae* GI.

of extrapolating correlative models.⁸ Dissimilar climate space between continents may have constrained the modelling projections presented here (Appendix S2). However, the CLIMEX models were able to project from the native occurrence points without these issues, reinforcing the importance both of comparing different modelling approaches and using physiologically based approaches (i.e. CLIMEX) when projecting to novel areas of climates as well.^{11,39} Distribution data for both *T. ostrinae* and *O. furnacalis* were limited because of recent survey efforts being restricted regionally and a lack of precise locality data associated with most published records.^{66,67} Our modelling approaches consider these two species in isolation, and inherently overlook competitive interactions with other *Trichogramma* species present across the distributions. Meta-analyses have suggested for competing natural enemy species that antagonism may result in effects on the target being less than additive, and this deleterious outcome is most obvious when the same life stage of a host is attacked.¹⁵ Therefore, any inference regarding areas suitable for *T. ostrinae* ought to be made with caution and requires empirical studies that include molecular identification of potential competing *Trichogramma* species that might have been incorrectly identified.^{23,68}

In terms of biological control, there are perhaps implications for areas with GI differences that favour the parasitoid over the host (Fig. 6a,c). Such areas may represent increased efficacy of the parasitoid wasp in those parts of Asia and North America and indicate areas with a higher probable success rate of inundative releases. In areas where *T. ostrinae* is in marginal climate space, the efficiency of biocontrol might be improved through increasing the number of wasps used in inundative releases.²¹ For example, Gagnon

*et al.*²⁶ recently reported that the use of *T. ostrinae* around Quebec (marginally suitable in our models) could effectively decrease the pressure exerted by ECB and its damage on sweet corn ears. Biocontrol efficiency might also be improved by timing releases to avoid extreme radiation/rainfall events based on meteorological forecasts. Better regional temporal forecasts should emerge by considering host–parasitoid relationships through dynamic population models that consider the interaction between trophic levels.

Under the future climate change scenarios investigated here, both ACB and *T. ostrinae* are expected to have broad geographical distribution in southeastern Asia into the next few decades. While this suggests a reasonable level of biological control potential for the future, there are also some likely challenges. The high degree of variation in life history traits within ACB populations across Asia,^{21,22} and the occurrence of multiple generations per year, could provide opportunities for rapid adaptation to novel environments.^{11,60} Areas representing a relative advantage for ECB through the central USA (Fig. 6d) contain low similarity to Asian climate space of *T. ostrinae* (Appendix S2), which might limit its control efficacy across central North America in the future. To sum up, the efficacy of *T. ostrinae* biocontrol across areas of northern USA and Canada is likely to be effectively improved under warming temperature around summer.^{26,61} Control efforts through the central North American area, in contrast, may be improved by increasing the numbers and release frequency of *T. ostrinae* and optimizing corn integrated control strategies based on further phenological dynamics studies.

Overall, the modelling approaches used here proved useful for examining broad-scale environmental limits to an egg parasitoid and its lepidopteran hosts. Global investigations provide

important hypotheses about key traits that limit distributions and define synchrony in host–parasitoid relationships. Such hypotheses can help to guide future experimental work to understand how climate change, such as climate seasonality/extremity, may affect these species at finer scales. We also identified areas potentially suitable for inundative releases; however, more regional-scale assessments will need to determine which strains of the hosts are present to determine how important life history traits such as diapause are represented in local populations. Finally, further phenological and diapause studies for *T. ostriniae* and its hosts are required to optimize corn integrated control strategies.

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SUPPORTING INFORMATION

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

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