

Projecting the Global Potential Distribution of *Cydia pomonella* (Lepidoptera: Tortricidae) Under Historical and RCP4.5 Climate Scenarios

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Abstract

The codling moth *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) is a destructive pest of apple (*Malus domestica* (Rosales: Rosaceae)), pear (*Pyrus* spp. (Rosales: Rosaceae)), and other pome tree fruits; outbreaks cause significant ecological and economic losses. In this study, we used CLIMEX model to predict and evaluate the global risk of *C. pomonella* based on historical climate data (1989–2018) and simulated future climate data (2071–2100) under the RCP4.5 scenarios. *Cydia pomonella* exhibited a wide distribution under both historical and future climate conditions. Climate change is predicted to expand the northern boundary of the potential distribution from approximately 60°N to 75°N. Temperature was the most dominant factor in climatic suitability for the pest. Combinations of multiple meteorological factors (relative humidity and precipitation) associated with a failure to break diapause in certain regions also affect suitability, particularly in northern South America and central Africa. Irrigation only had a slight impact on species favorability in some areas. The projections established in our study present insight into the global potential suitability of *C. pomonella* under climate change scenarios by the end of the 21st century. Farmers should be aware of the risk associated with the pest based on the results, which would provide guidance for quarantine agencies and trade negotiators worldwide.

Key words: Codling moth (*Cydia pomonella*), climate change, CLIMEX, potential distribution, pest management

The codling moth *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) is one of the most destructive pests of pome tree fruits in the world (Barnes et al. 1991). It is listed as a quarantine pest in many countries, including China, Japan, Germany, Britain, and Greece, where strict measures are taken to prevent its introduction and spread (Xiao 1993). *Cydia pomonella* originated in Europe and has spread to nearly 80 countries on six continents. The pest mainly attacks apples, as well as pears, Peaches (*Prunus persica* (Rosales: Rosaceae)), and apricots (*Prunus armeniaca* (Rosales: Rosaceae)), often causing devastating damage, especially to apples. *C. pomonella* has strong environmental adaptability (Cai et al. 2007). The international trade of fruits, packing materials, and other commodities (e.g., seeds and plant parts) can result in the inadvertent introduction of the pest outside of its native range (Kumar et al. 2015). Economic losses can mostly be attributed to damage caused by larvae (Du et al. 2012), which eat both the seeds and flesh of the fruit. The pupae continue to expand, exit the fruit, and sometimes hang in chains, resulting in substantial fruit drops and economic losses (Wang 2012). Infestation rates of *C. pomonella* are

generally above 50% (Shao et al. 2014), and can reach 90% in apple crops if orchards are not chemically protected (Brunner et al. 1982). Assuming a rate of 50%, the expected economic loss is 3.225 billion yuan per year in Xinjiang, China (Qin et al. 2006). Even with chemical pesticides, yields are reduced by 20–30%, and excessive pesticide use causes environmental pollution, and threatens the quality and safety of fruits (Wu et al. 2018).

According to the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5), the global average temperature is projected to increase 2°C and potentially 4°C by the end of the 21st century (IPCC 2014). Since 1901, average precipitation has increased in land areas of mid-northern latitude. By the end of this century, the average precipitation may decrease in many mid-latitude and subtropical arid regions, and increase in many mid-latitude humid regions. With the rise in the global average surface temperature, extreme precipitation events are likely to increase in intensity and frequency in most mid-latitude land areas and humid tropical regions (IPCC 2014). Previous studies have shown that temperature and precipitation can

significantly affect the physiology and spatial distribution of insects (Wolfe et al. 2008). In particular, temperature may influence populations of insects by altering the timing of emergence, rates of development, generation times, and the risk of invasion, with corresponding alterations in the geographical distribution (Rosenzweig et al. 2001, Trnka et al. 2007). Some insects will expand to higher latitudes and new regions in response to climate change (Bale et al. 2002). Many species have already responded to warming conditions over the last century (Crozier and Dwyer 2006). Moreover, the increased frequency of climate extremes can promote pest outbreaks (Gan 2004). Precipitation influences environmental humidity and the dynamics of insects, thereby affecting geographical distributions (Chang et al. 2008). In addition to precipitation, irrigation, another source of field water, affects the occurrence of species by influencing humidity and atmospheric conditions (Liang et al. 1998). Both the development and survival of species can be affected by irrigation in what would otherwise be an unfavorable dry season (Kriticos et al. 2015). Irrigation is essential for the growth of apples and other cash crops, and may influence the occurrence of *C. pomonella*.

Species distribution models (SDMs) are widely used to understand the relationships between species and their abiotic and biotic environments based on observations for ecological inference, or to test ecological or biogeographical hypotheses about species distributions and ranges. SDMs generally include two types: mechanistic and correlative (Pearson 2007). Mechanistic SDMs consider physiological constraints based on environmental factors, and correlative SDMs exploit the statistical association between occurrence data and spatial environmental data, assuming that the current distribution can effectively explain the ecological needs of species (Kearney et al. 2010). Many models have been developed to project the potential distributions of species under climate change scenarios owing to improvements in geographic information systems (GIS), including CLIMEX (Kriticos et al. 2015), DOMAIN (Carpenter et al. 1993), GARP (Stockwell 1999), and MaxEnt (Phillips et al. 2006).

Several SDMs have been applied to *C. pomonella*. Wu et al. (2018), Kumar et al. (2015), and Jiang et al. (2018) assessed the global risk of the establishment of the pest using CLIMEX and MaxEnt. CLIMEX has been used to build a distribution model for the *C. pomonella* in Norway by Rafoss and Sæthre (2003), and in China by Liang et al. (2010), the potential distribution of the pest has not been predicted on a global scale considering both climate change and irrigation patterns. And among SDMs, CLIMEX, as a semi-mechanistic approach for describing species responses to climatic variables at appropriate temporal scales, was well-suited to project potential distributions of the *C. pomonella* under climate change (Kriticos et al. 2015). The use of CLIMEX requires the biological information and known distribution data of the species involved. Given the published literature and database records, the information on *C. pomonella* is sufficient and can provide the required parameter values for modeling. We accounted for irrigation and used CLIMEX 4.0.0 based on historical (1989–2018) and future (2071–2100) climate data to identify the potential global distribution of *C. pomonella*. The prediction provides a reference for the development of prevention and control strategies for *C. pomonella* in global fruit production areas.

Materials and Methods

CLIMEX Model

To predict the global potential distribution of *C. pomonella*, CLIMEX 4.0.0 (Hearne Scientific Software, Melbourne, Australia)

was used. CLIMEX combines the growth index (GI), reflecting conditions during the growing season, and the stress index (SI), describing the cumulative effects of stresses during the inclement season into an overall ecoclimatic index (EI), with values ranging from 0 to 100. And the EI describes the potential for population growth, with the annual stresses that limit survival and with any limiting factors, such as diapause. EI values close to 0 indicate that a location is not favorable for the long-term survival of a species, while an EI value of 100 is only achievable under ideal conditions (Kriticos et al. 2015). For a detailed description of CLIMEX, please refer to (Kriticos et al. 2015).

ArcGIS Software

The Spatial Analyst Module of ArcMap 10.6, developed by the US Environment Systems Research Institute (ESRI 2020), was used to analyze the projections obtained using CLIMEX. The inverse distance weighted interpolation (IDW) function was used to visualize the results for the species under historical and future climate conditions.

Known Distribution of *C. pomonella*

Information for the current global distribution of *C. pomonella* was obtained from the European and Mediterranean Plant Protection Organization (EPPO), Global Biodiversity Information Facility (GBIF), and Centre for Agriculture and Bioscience International (CABI) databases and the literature (CABI 2019, EPPO 2019, GBIF 2019). We searched literature with codling moth/*Cydia pomonella* as keywords, and went through all the articles related to the species to collect distributional information, including where the experimental insects were collected. If the longitude and latitude information was clearly recorded in the literature, it was directly quoted; if only a certain range of the distribution was known, the location of the smallest geographic unit of the range was used to indicate its distribution. *C. pomonella* was widely distributed across all continents except Antarctica. Total occurrence records are presented in Fig. 1.

Climate Data

Historical climate data (1989–2018) were obtained from the gridded Climatic Research Unit (CRU) Time-series (TS) version 4.01, with a high-resolution (0.5° latitude, 0.5° longitude) grid produced by CRU at the University of East Anglia (Harris and Jones 2017). Five meteorological parameters (average monthly minimum and maximum temperatures, average monthly rainfall, and average relative humidity at 09:00 a.m. and 15:00 p.m.) were extracted for 1989–2018 as historical climate data using CLIMEX (Kriticos et al. 2012).

Considering different combinations of economic, technological, demographic, policy, and institutional factors, Representative Concentration Pathways (RCPs, RCP2.6, RCP4.5, RCP6.0, and RCP8.5) from Coupled Model Intercomparison Project Phase 5 (CMIP5) describe future greenhouse gas emissions conditions. The period 2071–2100 under RCP4.5 was chosen as the future climate scenario. To capture the impact of future climate change on the potential distribution, a relatively longer time period at the end of this century (2071–2100) was selected for predictions. Additionally, based on commitments to controlling carbon emissions to mitigate climate warming, predictions for the temperature rise by the end of the century in the RCP8.5 scenario may be too extreme (i.e., exceeding 4°C), while RCP2.6 predictions are too minor (i.e., unlikely to exceed 2°C) (IPCC 2014). Furthermore, projections more closely resemble observations when using the multi-model than the single model (Hu and Ren 2016, Zhang et al. 2016), and there are fewer

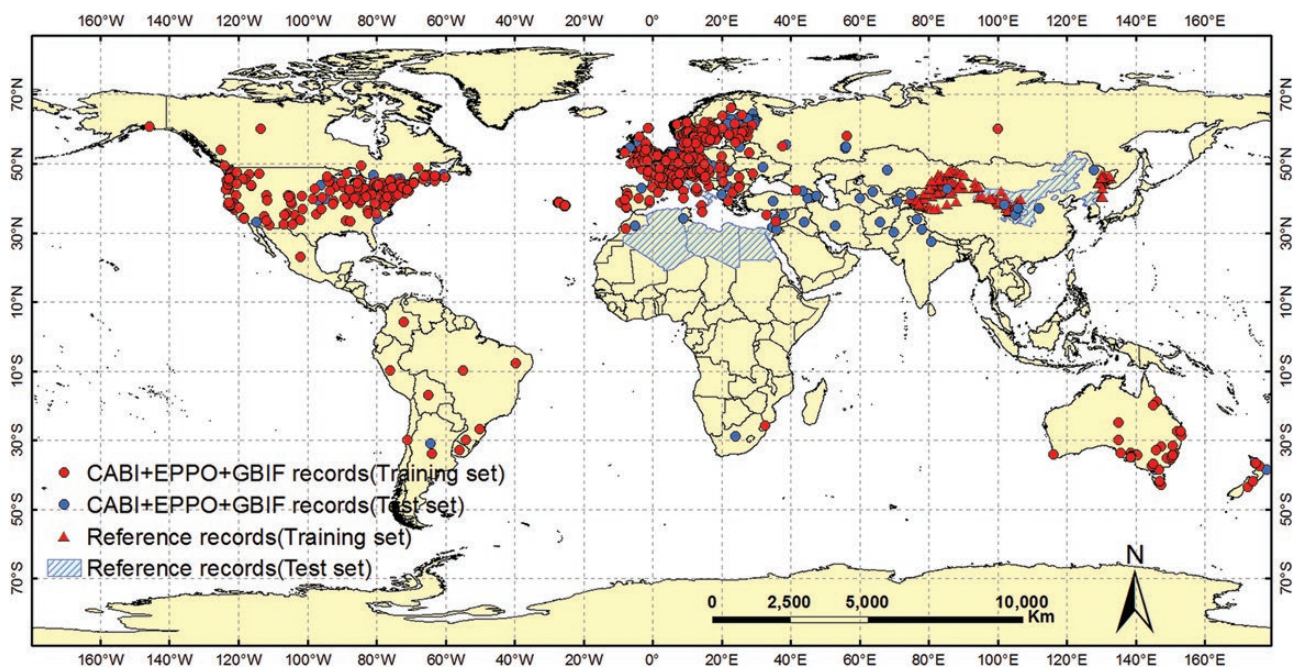


Fig. 1. Known geographical distribution of *Cydia pomonella*. Red circles and red triangles indicate regions selected for the training set; blue circles and blue shadows indicate regions selected for validation. Points represent distribution records from the CABI, EPPO, and GBIF databases; triangles and shadows represent distribution records obtained from the literature.

related models of RCP6.0. Accordingly, the RCP4.5 stabilization scenario was finally chosen. We also followed Zou et al. (2020) in our study, who used 29 general circulation models and applied the same scenario for future climate data. Additional details regarding the climate data can be found in Zou et al. (2020)

Irrigation Data

To consider the effects of irrigation, a composite map of irrigated and unirrigated areas generated by Siebert et al. (2013) was used to visualize the overall projected suitability for *C. pomonella*. First, the 1.5 mm day^{-1} in summer irrigation scenario from CLIMEX was applied. Then we developed the composite map according to the Global Map of Irrigation Areas. The EI for the un-irrigated scenario was used in areas without irrigation, and EI for 1.5 mm day^{-1} in the summer irrigation scenario was mapped in areas under irrigation. The global irrigation areas were obtained from the Food and Agriculture Organization of the United Nations (Siebert et al. 2013).

Fitting CLIMEX Parameters

Some scholars have used CLIMEX to predict the potential distribution of *C. pomonella* (Rafoss and Sæthre 2003, Liang et al. 2010, Kumar et al. 2015, Wu et al. 2018), and CLIMEX also considered *C. pomonella* as an example to list the parameters (Kriticos et al. 2015). However, the prediction results of these parameters did not cover all currently known species distributions well (without the known distribution of the *C. pomonella* between the 20th parallels), which may be due to the updated known occurrence records of the species in recent years. While adjusting the parameter values, 70% of the occurrence records were randomly selected from the total known distribution as the training set, and the remaining 30% of records were used as the test set. For reference, the parameters in the previous research and the CLIMEX template, and the final parameter values after adjustment are listed in Table 1. The detailed information for specific parameters were modified as follows.

Growth indices (GI)

CLIMEX uses the annual growth index (GI_A) scaled from 0 to 1 to describe conditions that favor population growth. The index usually combines the response to temperature, soil moisture, relevant day lengths, and diapause for the species (Kriticos et al. 2015).

Temperature index (TI)

Four parameters were used to define temperature suitability: the lower temperature threshold (DV0), the lower optimum temperature (DV1), the upper optimum temperature (DV2), and the upper temperature threshold (DV3). Liu et al. (2011) reported that the lower developmental thresholds of the egg, larva, and pupa are 10.64, 10.68, and 9.33°C, respectively. Howell and Neven (2000) found that the optimal temperature for *C. pomonella* development is 14.8–29.6°C. Therefore, DV2 was set as 30°C; DV0 and DV1 were set as 9°C and 15°C, respectively, which were consistent with the parameters in previous research (Rafoss and Sæthre 2003, Liang et al. 2010, Kriticos et al. 2015, Kumar et al. 2015, Wu et al. 2018). Temperatures exceeding 33°C block growth according to Aghdam et al. (2009), so DV3 was set as 34°C.

Moisture index (MI)

The lower soil moisture threshold (SM0), lower optimal soil moisture (SM1), upper optimal soil moisture (SM2), and upper soil moisture threshold (SM3) were used to define the MI. Owing to the limited information regarding the soil moisture requirements of *C. pomonella*, appropriate parameters were determined based on known distributions. Moisture indices consequently remained the same as in Kumar et al. (2015).

Diapause index (DI)

Diapause is an adaptation that enables a species to withstand prolonged periods of unfavorable conditions. DI was defined by the diapause induction day length (DPD0), diapause induction temperature

Table 1. CLIMEX parameter values for *Cydia pomonella*

Parameters	Descriptions	Value						
		Skarratt et al. (1995)	Rafoss and Sæthre (2003)	Liang et al. (2010)	Kumar et al. (2015)	Wu et al. (2018)	CLIMEX template (Kriticos et al. 2015)	Final parameters
Moisture								
SM0	Lower soil moisture threshold ^a	0.2	0.1	0.02	0.02	0.02	0.1	0.02
SM1	Lower optimum soil moisture ^a	0.5	0.3	0.3	0.1	0.3	0.2	0.1
SM2	Upper optimum soil moisture ^a	1.5	1.5	1	1.8	1	1	1.8
SM3	Upper soil moisture threshold ^a	2.5	2.5	1.5	2.5	1.5	1.2	2.5
Temperature								
DV0	Lower threshold (°C)	2	9	9	9	9	10	9
DV1	Lower optimum temperature (°C)	17	15	15	15	15	20	15
DV2	Upper optimum temperature (°C)	22	27	30	27	31	30	30
DV3	Upper threshold (°C)	25	30	33	34.4	34	33	34
Light								
LT1	Day length below which growth is zero (h)	—	—	—	13.5	—	—	—
LT0	Day length above which growth is maximum (h)	—	—	—	15.5	—	—	—
Cold Stress								
TTCS	Cold stress temperature threshold (°C)	5	1	—	-15	—	—	—
THCS	Cold stress temperature rate (week ⁻¹)	0.00001	0.00001	—	-0.0001	—	—	—
Heat Stress								
TTHS	Heat stress temperature threshold (°C)	29	35	35	35	35	33	35
THHS	Heat stress temperature rate (week ⁻¹)	0.006	0.006	0.002	0.0001	0.002	0.0003	0.0001
Dry Stress								
SMDS	Soil moisture dry stress threshold ^a	0.15	0.15	0.02	0.02	0.02	0.1	0.02
HDS	Stress accumulation rate (week ⁻¹)	0.01	0.01	-0.005	-0	-0.01	0.003	-0.005
Wet Stress								
SMWS	Soil moisture wet stress threshold ^a	2	2	1.5	2.5	1.5	1.2	2.5
HWS	Stress accumulation rate (week ⁻¹)	0.002	0.002	0.003	0.002	0.003	0.0005	0.002
Diapause								
DPD0	Diapause induction day length (h)	12	0	—	15	—	14	11.8
DPT0	Diapause induction temperature (°C)	10	5	11	11	—	11	22
DPT1	Diapause termination temperature (°C)	0	0	6	6	—	6	8
DPD	Diapause development days (d)	0	90	90	90	—	90	100
DPSW	Diapause summer or winter indicator	—	—	—	0	—	0	0
Hot-Wet Stress								
TTHW	Hot-Wet temperature threshold ^a	—	—	25	—	25	—	—
MTHW	Hot-Wet moisture threshold ^a	—	—	0.7	—	0.7	—	—
PHW	Stress accumulation rate (week ⁻¹)	—	—	0.035	—	0.035	—	—
Threshold Heat Sum								
PDD	Effective accumulated temperature (degree-days)	750	580	450	580	450	450	450
Irrigation scenario								
							1.5mm day ⁻¹ in summer	1.5mm day ⁻¹ in summer

^aThreshold without units is expressed as the proportion of holding capacity for soil moisture. (0 indicates oven-dried and 1 indicates field capacity (saturation)). Values over 1 indicate potentially excessive rainfall and soil moisture.

(DPT0), diapause termination temperature (DPT1), diapause development days (DPD), and diapause summer or winter indicator (DPSW) (Kriticos *et al.* 2015). DPD0 and DPT0 were set as 11.8 h and 22°C, respectively, based on Dyck (2010), who observed that a day length of 8–12 h and 15–25°C for no less than 12 h can effectively induce diapause. Liu *et al.* (2017) reported that low temperature was the key factor to break the diapause of *C. pomonella*; accordingly, DPT1 was set as 8°C to guarantee the known distribution in India. Since Ashby and Singh (1990) recommended that a 100-day conditioning period could terminate diapause in *C. pomonella* larvae, DPD was set as 100. In addition, DPSW was set as 0, referring to winter diapause (Liu *et al.* 2015).

Stress indices

The stress indices in CLIMEX are set to limit species survival during adverse seasonal conditions and to determine the geographical distribution. An annual stress value of 100 is lethal and precludes a species from persisting in the given location. And a value of 0 indicates a lack of stress at the location (Kriticos *et al.* 2015).

Heat stress (HS)

Assuming the degree-day model of HS accumulation, the heat stress temperature threshold (TTHS) and heat stress temperature rate (THHS) define the HS in CLIMEX. Kriticos *et al.* (2015) indicated that the TTHS must be equal to or greater than DV3, since HS cannot accumulate within the suitable temperature range for development. Thus, the TTHS parameter was set as 35°C; additionally, THHS was set as 0.0001 week⁻¹ according to Kumar *et al.* (2015).

Dry stress (DS)

DS is defined by the dry stress threshold (SMDS) and dry stress accumulation rate (HDS). The dry stress threshold (SMDS) was set to the same value as SM0, since dry stress only begins to accumulate when soil moisture drops below SM0 (Kriticos *et al.* 2015). HDS was set to 0.005 week⁻¹ to match *C. pomonella* occurrences in some dry regions of India.

Wet stress (WS)

WS is defined by the soil moisture wet stress threshold (SMWS) and stress accumulation rate (HWS), which constrain the species distribution in the case of excessive soil moisture (Kriticos *et al.* 2015). SMWS was set as 2.5 to match SM3, and HWS was set as 0.002 week⁻¹ based on Kumar *et al.* (2015) to describe the humidity conditions tolerated by the species.

Effective degree-days (PDD)

For an excellent fitting to the current distribution, the PDD was set as 450 degree-days, which were also consistent with the parameters in previous research (Liang *et al.* 2010, Kriticos *et al.* 2015, Wu *et al.* 2018). This ensured a consistent number of generations for the pest in the model and the actual situation. The *C. pomonella* exhibits one generation per year in northern Europe, three or four generations per year in southern Europe and two or three generations per year in northwest China (Zhai 2009, Xu *et al.* 2012).

Classification of EI Values

EI values for climate suitability vary among species. The potential distribution of a species is usually divided into four types: unsuitable, marginal, favorable, and very favorable. In this study, the critical values for the suitability categories for *C. pomonella* were mainly based on

occurrence records. Moreover, Sutherst (2003) suggested that EI < 10 indicates that a location is marginal for survival, and EI values exceeding 20 have been found to support substantial population densities. *Cydia pomonella* is native to southeastern Europe and is now widespread throughout Europe, with severe outbreaks (Kumar *et al.* 2015). Therefore, these areas were considered as very favorable regions for the pest. Considering the EI values of these areas are all greater than 20, combined with the statement of Sutherst (2003), and the final cut-off between favorable and very favorable was adjusted. According to Sutherst (2003) and reported outbreaks, the cut-off for other types of regions were adjusted. Four groups of EI values were defined as follows: unsuitable (EI = 0), marginal (0 < EI ≤ 10), favorable (10 < EI ≤ 20), and very favorable (EI > 20).

Analysis of Results

A composite map with the irrigation areas reported by Siebert *et al.* (2013) was used as the foundation for the study. First, the potential global distribution of *C. pomonella* under historical and future RCP4.5 scenarios was predicted. Then, the impacts of climate change on the species distribution were assessed by comparing areas with different degrees of suitability, including differences in the suitable range. Variation in climatic favorability among latitudes was also performed following Ge *et al.* (2019), that is, calculating the average EI values of all climatic stations from CLIMEX at different latitudes. In addition, the driving meteorological variables limiting the occurrence of *C. pomonella*, the relationship between these factors and climate change, and the effect of these factors on the occurrence of the *C. pomonella* were explored.

Results

Predicted Potential Distribution of *C. pomonella* With Composite Irrigation Under Historical Climate Conditions

In the historical scenario, the potential global distribution of *C. pomonella* was predicted under composite irrigation (Fig. 2A). All occurrence records in the test set (Fig. 1) were located within the projected potential distribution (Fig. 2A), showing that our model fits the actual occurrence records with a high degree of accuracy.

As shown in Figs. 2A and 3, most areas between 50°S and 68°N are suitable for *C. pomonella*, including 55.55% of the global land mass, excluding parts of northern South America, central Africa, central India, southwestern China and northwestern Oceania. In particular, very favorable areas accounted for a large portion (53.27%) of the suitable areas. Besides, the marginal and favorable regions accounted for 32.55% and 14.19% of the total potential distribution, respectively.

Predicted Potential Distribution of *C. pomonella* Under the RCP4.5 Scenarios

The potential global distribution of *C. pomonella* without irrigation was predicted under the RCP4.5 scenario for 2071–2100 (Fig. 2B). Overall, the northern boundary of the potential distribution would expand northward under the climate change scenario, from approximately 68°N to 75°N, and the southern border of suitable regions would expand southward 5° (up to 55°S) compared to the historical condition. To further explore the impacts of climate change on the potential distribution, we evaluated changes in various types of regions (from unsuitable to very favorable) (Fig. 3) and regional changes (Fig. 4).

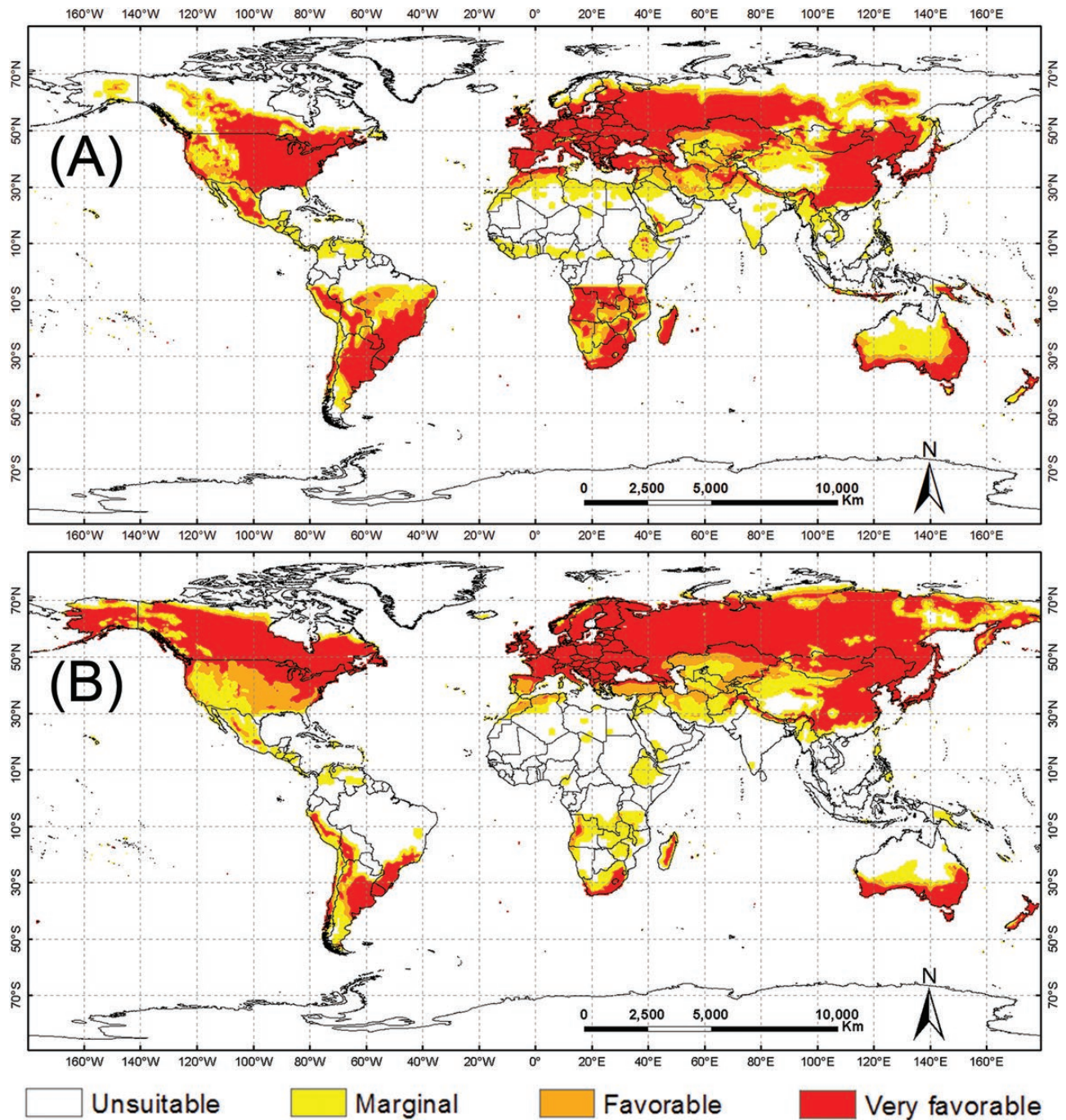


Fig. 2. Projected potential distribution for *C. pomonella* under different climate scenarios. Projected potential global distribution of *C. pomonella* under (A) historical climate scenario with composite irrigation, and (B) future climate scenarios without irrigation. White regions are unsuitable for *C. pomonella* (EI (climatic suitability) = 0), yellow indicates marginal regions ($0 < EI \leq 10$), electron gold indicates favorable regions ($10 < EI \leq 20$), and red indicates very favorable regions ($EI > 20$).

The whole unsuitable area under the RCP4.5 scenario was 3.46% less than that under historical climate conditions. Regional changes in unsuitable areas were mainly observed in Mexico, northern South America (mainly Brazil), Africa, India, and central Oceania, concentrated between 30°S to 30°N. Contrary to the future scenario, new unsuitable regions under historical conditions were concentrated in the north of 60°N, mainly in northern North America and Russia.

Under future climate conditions, the predicted area of marginal regions occupied 14.62% of the total land area and 24.78% of the

total potential distribution. The potential area for *C. pomonella* was 8.77% lower in the future than in historical scenarios. Areas where significant decreases were predicted in the future scenario include eastern South America (mainly Brazil), central Oceania, and northern Africa. In addition, marginal regions would increase in southern North America and parts of southern Africa, while very favorable regions in parts of those areas would transform into marginal regions.

Although the distributions of favorable regions were different under historical and future conditions, the total area was almost the

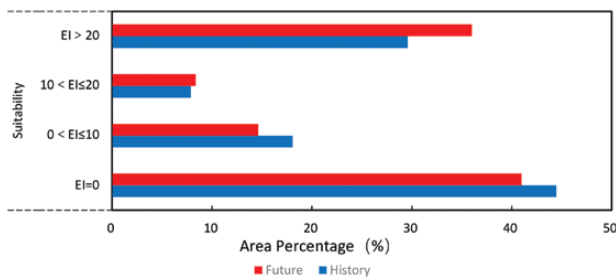


Fig. 3. Relative areas of regions of different climatic suitability for *C. pomonella* under historical (1989–2018) and future (2071–2100) climatic conditions.

same. The area of favorable regions was 8.37% of the total land area, which was almost similar to that under historical conditions (7.88%). Regional changes in favorable areas were clearly observed in southern North America (the United States), central Asia (Turkey, Iran, Afghanistan, Kazakhstan, and Mongolia) and northern Russia by the end of the 21st century. In addition, new favorable regions under historical scenario were concentrated in central Brazil, southern Africa (Namibia, Republic of South Africa, Zambia, and Tanzania), and central Russia.

An increase in the potential distribution of *C. pomonella* would be related to an increase of very favorable regions. The very favorable regions were concentrated in northern North America and northern Asia under the RCP4.5 scenario, representing 36.02% of the total land area and 61.04% of the total potential distribution. Moreover, the very favorable regions in the future scenario would increase by 6.43% when compared with those under historical climate conditions. Compared with the past, the very favorable regions between 30°N–50°N and 10°S–30°S were reduced to varying degrees, while almost all regions between 50°N and 70°N were highly adaptable for *C. pomonella*.

Differences in EI values between historical and future climate scenarios were mapped, and the variation among latitudes were also evaluated (Fig. 5). We identified 50°N as a boundary area; in the north of 50°N, most regions would exhibit an increase in suitability, whereas the opposite trend was predicted in the south of 50°N. In addition, the degree of change was greatest between 60°N–75°N and 5°S–30°S; and all areas where suitability expanded northward were highly suitable for *C. pomonella* survival. In general, the potential global distribution of the species would increase. These results are mainly driven by the reductions in unsuitable areas between 10°S–30°S, and the increase in very favorable regions mentioned above.

Driving Variables

Based on the EI formula, *C. pomonella* is unable to survive when $GI = 0$ or $SI \geq 100$ (Kriticos et al. 2015). According to the CLIMEX results, we found that the EI values were largely determined by changes in meteorological factors, especially temperature and HS. Diapause was also a major factor which restricted EI values. Figures 6 and 7 summarize the limited suitability (EI = 0) in specific locations, and Supp Fig. S1 (online only) summarizes changes in suitability caused by climate change.

Within GI, temperature and diapause were the main factors restricting the survival of *C. pomonella* in Greenland under both historical and future climate conditions. In addition to Greenland, some regions in northern North America (the United States and Canada), northern South America, central Africa, northern Russia,

southwestern China, and eastern India were also limited by diapause, under historical conditions (Fig. 7C). In the future scenario, diapause-restricted areas would increase between 30°S–30°N, and decrease between 50°N–70°N. Overall, with climate change, the restrictions related to temperature would increase while limitations related to diapause would decrease. The impacts of stress indices on habitat suitability were relatively minor, and climate change would strengthen their restrictive effects. The suitability of scattered regions in central Africa, the western border of Mexico, and central South America was reduced by HS or with other factors in the future. While the stress indices did not pose a threat to the survival of the *C. pomonella* under historical conditions.

Discussion

Appropriate models for the potential distribution of quarantine pests are urgently needed for pest risk assessments. Differences in projected distributions among studies can be explained by a wide range of factors, including differences in known distribution records, parameter selections and settings, climate data, and analysis software. Suitable areas for the *C. pomonella* were greater in our model than in previously developed models, and this difference may be explained by our inclusion of additional occurrence records and any of the considerations mentioned above. Differences between the results of Liang et al. (2010) and our study can be explained by the underestimation of potential distributions using the regional model, which did not include all environmental conditions where *C. pomonella* occurs. This may also explain the predictions of the regional model of Rafoss and Sæthre (2003) in Norway. Furthermore, the parameter settings for CLIMEX differed among studies. Unlike Wu et al. (2018) and Liang et al. (2010), we added the diapause parameter in our model, which is also a characteristic of the *C. pomonella* (Wu et al. 2015). In addition, different climate data would lead to differences in projections, even with the same CLIMEX parameters. Disagreements between CLIMEX and MaxEnt in Kumar et al. (2015) may be due to differences in the types and spatial resolutions of climatic datasets, levels of complexity in model fitting, and specific assumptions (Elith et al. 2011, Kriticos et al. 2015).

The results of CLIMEX model between our study and Kumar et al. (2015) are mainly reflected in the prediction between 20°N and 20°S. We believe that probably based on the updated known distribution of the *C. pomonella* in recent years, some predicted areas within these regions are suitable for the survival of the species after modeling in our study; and Kumar et al. (2015) model did not predict these areas as suitable based on the distribution records at that time. In addition, another obvious difference is concentrated between 30°S and 50°S, the southern United States and southeastern China. In Kumar's model, these regions are mostly marginal and moderately suitable for *C. pomonella*, while most of them are highly favorable in our model. Our study is most similar to Wu et al. (2018) among all the previous research, which both have analyzed the current and future species distribution on a global scale, although the selected climate scenarios and predicted years are different. As far as the results are concerned, Wu's description of the world is more general, which seems to focus on China, and there is no figure to assist in the explanation. With the resulting charts, our study provides a more detailed analysis of the global potential distribution of *C. pomonella* and the reasons for these differences among different regions. The results obtained within our study are consistent with Wu et al. (2018) on the whole, but there are still discrepancies. Under historical climatic conditions,

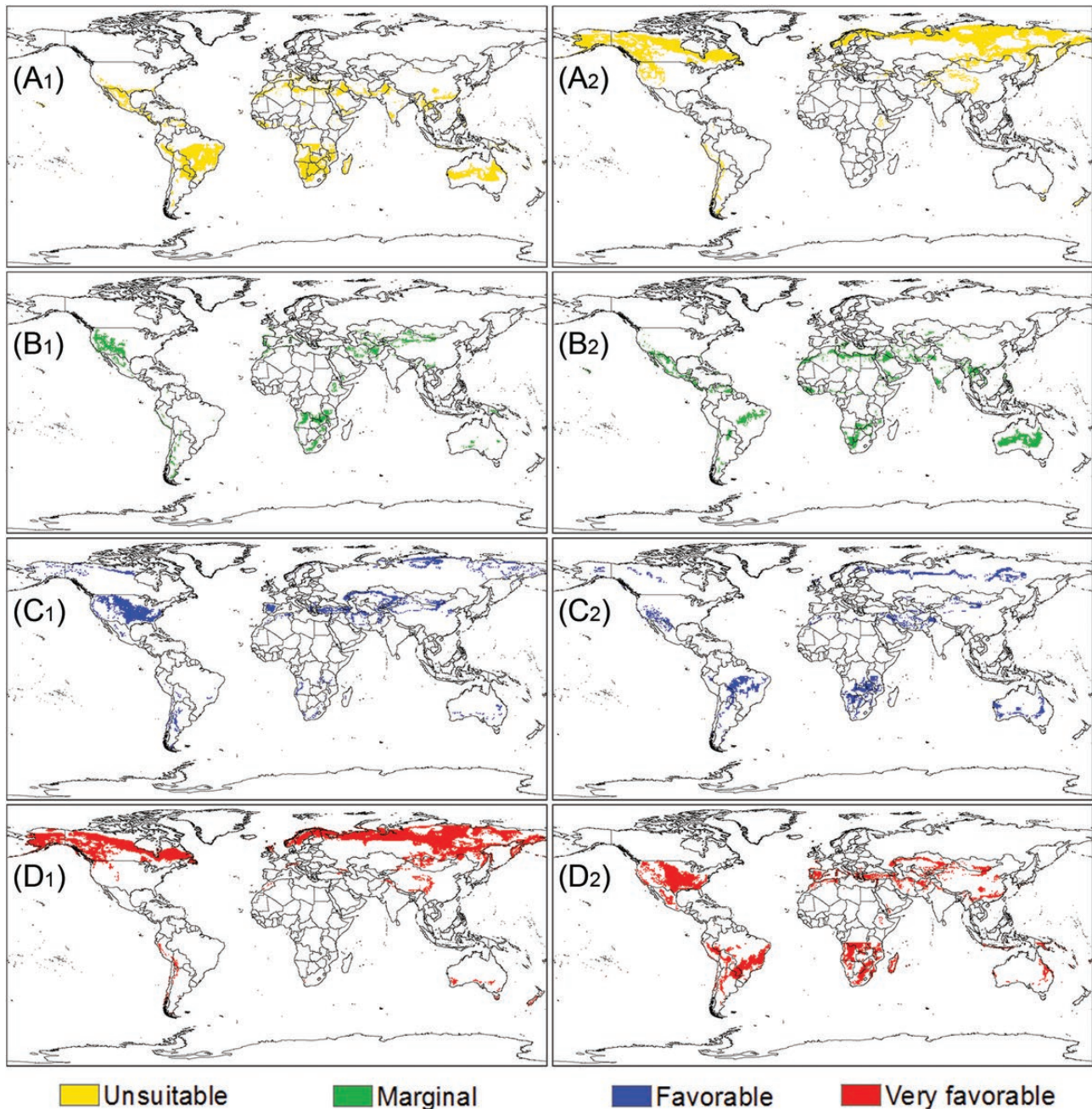


Fig. 4. Regional changes in four types of climatic suitability of *C. pomonella* over time. A (yellow regions), B (green regions), C (blue regions), and D (red regions) indicate new areas of unsuitable, marginal, favorable, and very favorable climatic suitability, respectively. Subscript 1 indicates the future region other than the overlapping part of history and future, and subscript 2 indicates the historical region other than the overlapping part of history and future.

the coastal areas of Chile and Peru are highly favorable according to Wu et al. (2018), while in our study they are marginal areas for the *C. pomonella*; Honduras, Guatemala, Nicaragua, Costa Rica, and Panama, which are adjacent to southern Mexico, are mostly unsuitable in Wu et al. (2018), while the situation is opposite in our model. Given that their results are not displayed by geographic maps, and the suitability of areas is unknown, no further comparisons are possible. Furthermore, most hosts of the *C. pomonella* need to be irrigated as economic crops, so we thought it is necessary to take the irrigation factor into account. And this is the main difference between our model and all the existing studies.

Our results showed that meteorological factors would be affected by climate change, leading to changes in climatic suitability in various regions. And in summary, the *C. pomonella* tends to spread to higher latitudes where its European origin is located with climate change. The decline in the EI difference, mainly detected in the south of 50°N between future and historical climate conditions, was probably due to decreases in temperature, moisture and diapause indices. Between 50°N and 70°N, climatic suitability increased as a result of a rise in temperature; and maybe because of temperature, DI is no longer a limiting factor in these areas (Fig. 7, Supp Fig. S1 [online only]). In Canada and Russia,

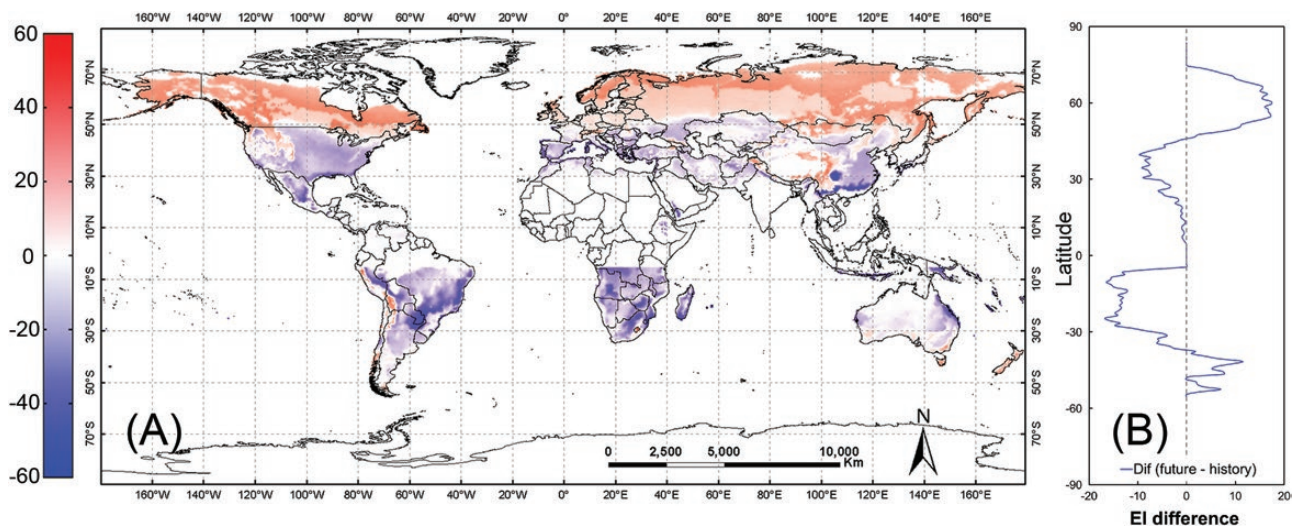


Fig. 5. Effects of climate change on climatic suitability for *C. pomonella*. (A) Global changes in EI differences between historical (1989–2018) and future (2071–2100) climate conditions. Red indicates an increase, blue indicates a decrease, and the color gradation indicates the degree of change in EI values. (B) Changes in the EI difference among latitudes.

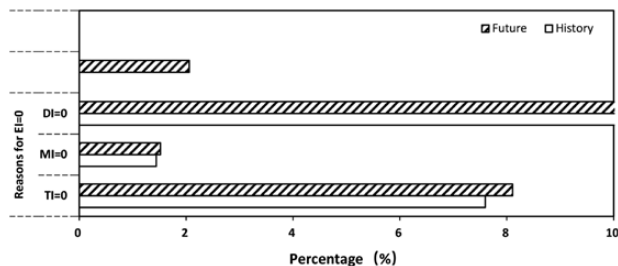


Fig. 6. Contribution of four meteorological factors to "EI = 0" for *C. pomonella* under current and future climate scenarios.

where the winter temperature is relatively low, a considerable portion of larvae can safely overwinter under the protection of snow (Putman 1963), and the temperature rise caused by future climate change will be more conducive to species survival, explaining the northward shift of the suitable boundary in terms of temperature for the *C. pomonella*. In particular, areas identified as unsuitable for the *C. pomonella* in the historical scenario would become suitable (between 60°N and 75°N), while areas with higher average annual temperatures previously would become unsuitable or marginal (e.g., Brazil and Africa) due to the decreases in temperature, moisture, and effects of diapause with climate change. Our model did not predict favorable suitability in most parts of India, southwestern China, and northern and central Oceania primarily because the combination of temperature and humidity in these areas did not satisfy the requirements for the *C. pomonella* to break diapause. Increased HS also causes a decreased suitability in northern Brazil, northern Africa and Oceania.

Precipitation is also directly related to the temperature and humidity in specific areas, and affects climatic suitability. Climate change has similar effects on rainfall and temperature, except in southern North America, central Africa and southwestern China, where precipitation increases while temperature decreases. Supp Fig. S2 (online only) shows that climate change would increase precipitation in areas north of 30°N. Thus, we inferred that the combined effect of precipitation and other meteorological factors (mainly temperature) expanded and intensified the suitable regions in that area.

Studies have shown that agricultural irrigation has little impact on the global average temperature (Sacks et al. 2009), but has a significant cooling effect on the regional atmosphere (Lobell et al. 2006). Thus, from another perspective, irrigation has indirect effects on suitability via its influence on precipitation. We evaluated the effects of irrigation on species occurrence by comparing with the predicted suitability under natural rainfall (Supp Figs. S3 [online only], Fig. 4). Although irrigation only had a slight impact on the potential distribution of the pest, we can still see that under historical conditions, parts of marginal regions in the United States, Turkey, Iran, and Afghanistan would change into favorable when irrigation was considered. In addition, suitable regions in Mexico, Portugal, Spain, and northwestern China would increase after irrigation (Supp Fig. S4 [online only]). In the future, the above-mentioned areas will undergo the same changes as observed under the historical scenario after irrigation, with a smaller degree of change. The differences between future and historical patterns may be explained by the effects of climate change and irrigation on various parameters, consequently altering the climatic suitability. And irrigation appears to be more responsible for the difference in EI in some areas, like the western United States, where the suitability is increased while not receiving significant rainfall. However, there are some limitations of irrigation scenarios we applied in our study. Firstly, we were only able to identify where irrigation has been applied in the world, but were not able to obtain the specific amount of irrigation. Secondly, as the global precipitation patterns are predicted to be affected by climate change (IPCC 2014), the range and distribution of irrigated regions under future and historical conditions may not be completely consistent. These issues may impact the study outcomes and predicted distributions.

Overall, the known occurrence of the *C. pomonella* is spread across all continents (except Antarctica), mainly including southern North America (the United States), central Asia and almost all countries in Europe. Compared with the predicted results under the current climate scenario, the pest has not spread to all potential areas actually. While with climate change, the actual global distribution of the *C. pomonella* may further expand in the future. At present, the pest is less distributed in some areas, but it will continue to spread due to climate change, such as Canada and Russia. On the contrary,

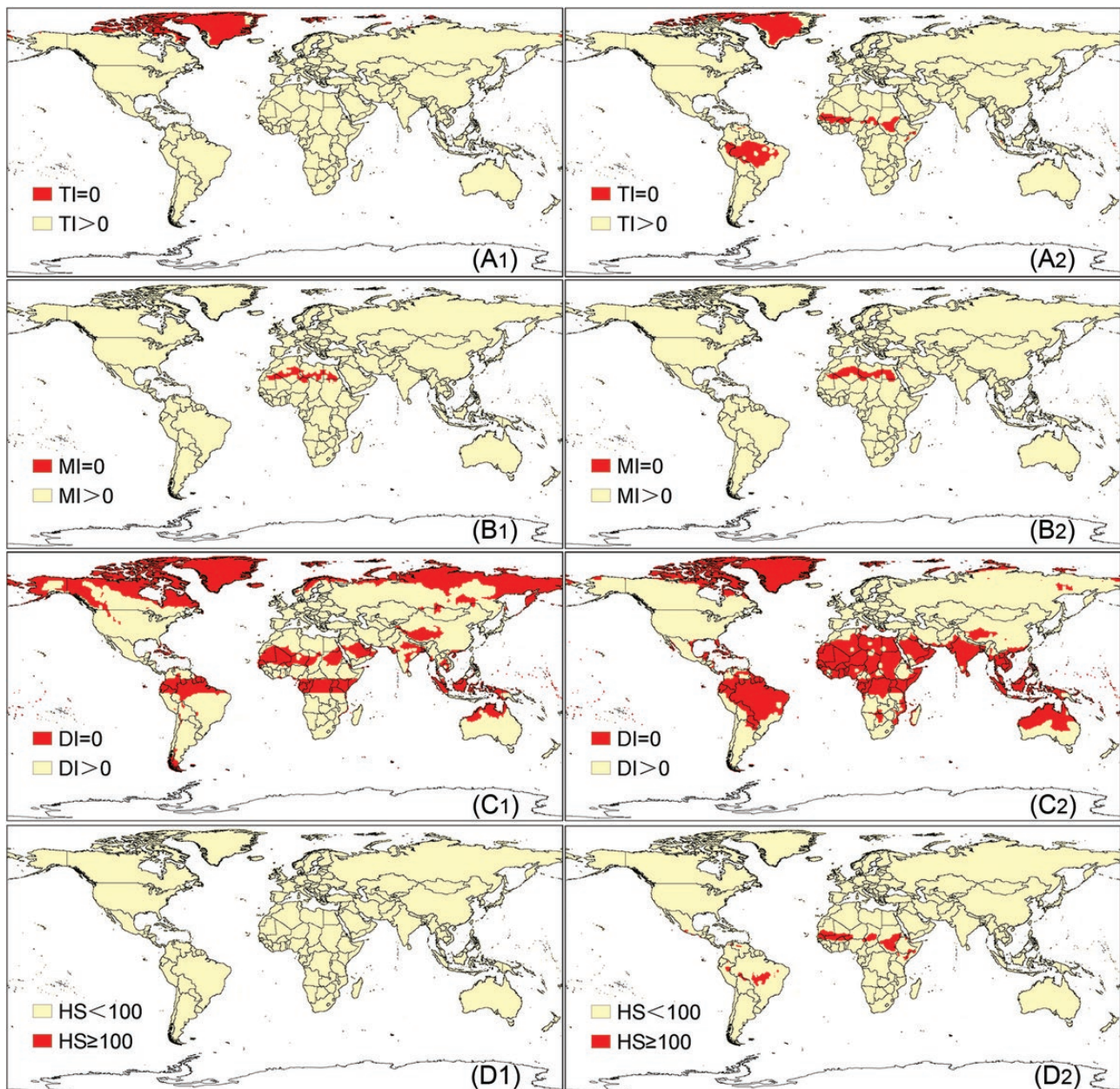


Fig. 7. Distribution maps of four meteorological limiting factors for *C. pomonella*. Red areas in A, B, C, and D represent regions where the temperature index (TI), moisture index (MI), diapause index (DI), and heat stress index (HS) will be unsuitable for *C. pomonella*, respectively. Subscripts 1 and 2 indicate historical and future climate scenarios.

although some areas are currently infested by the *C. pomonella*, the climate of these areas may not be suitable enough to support the survival of the pest in the future, such as the central part of Brazil, Queensland and the Northern Territory in Australia. In addition, there are still some regions that do not have exact known distribution records, but are predicted to be favorable in our model. This may be because the pest's damage has not been recognized or detected, or it has not yet spread although the area is suitable for *C. pomonella* survival. For example, the pest in Mexico may spread south to Guatemala, Honduras, Nicaragua, Salvador, Costa Rica, and Panama, where no *C. pomonella* are currently distributed; Ethiopia and other central African countries, as well as southeastern China, are likely endangered by the pest of neighbors with its natural expansion.

Our projections are useful for the identification of potential suitable areas for the *C. pomonella* and the long-term quarantine of the pest under climate change. However, in addition to meteorological factors, biotic interactions (e.g., host and predator availability) can also affect species establishment (Baker et al. 2000, Shabani et al. 2012). Dozens of fruit hosts of the *C. pomonella* are distributed worldwide, and characteristic changes may lead to adaptation to new hosts, so the influence of hosts was ignored in this study. Natural enemies of the *C. pomonella* like the trichogrammatidae, granulosis virus, and woodpeckers are also threats for *C. pomonella*, but it is impossible to obtain records for natural or artificially cultivated enemies in the known distribution, making it difficult to evaluate associations between enemies and *C. pomonella* occurrence (Biache et al. 2000, Quarles 2000, Loesel et al. 2010). Thus, we did

not consider the role of enemies. These may explain instances of predicted climatic suitability in several areas where the *C. pomonella* currently does not occur. Furthermore, we ignored species evolution. The model parameters will change according to the adaptation of the species to the environment over time, and key biological characteristics vary among regions. Moreover, land use, soil type, and human activities should be considered in the future to further improve the accuracy of the results.

Conclusions

In summary, climate change will shift the potential distribution of *C. pomonella* to varying degrees in different regions. Climatic suitability will increase mostly in regions north of 50°N (50°N to 75°N) and will decrease in regions south of 50°N (50°N to 40°S) under climate change scenarios. Furthermore, average annual temperature is most dominant factor influencing the potential global distribution of *C. pomonella* when compared with relative humidity and precipitation. The combined effect of multiple meteorological factors related to a failure to break diapause is also a major determinant of suitability. The projections developed in our study clarify the potential suitability of *C. pomonella* due to climate change by the end of the 21st century at a global scale. These results can support region-specific monitoring efforts and decision-making by quarantine agencies and trade negotiators.

Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

Supplementary Fig. 1. Effects of climate change on factors that limit the potential distribution of *C. pomonella*.

Supplementary Fig. 2. Impacts of climate change on monthly average precipitation.

Supplementary Fig. 3. Potential global distribution of *C. pomonella* with different irrigation scenarios under historical and future climate conditions.

Supplementary Fig. 4. Differences in climate suitability under composite irrigation and natural rainfall scenarios.

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Author Contributions

Conceptualization, X.G. and S.Z.; Data curation, S.G., Y.Z. (Ya Zou), Y.Z. (Yuting Zhou) and T.W.; Formal analysis, S.G., Y.Z. (Ya Zou) and Y.Z. (Yuting Zhou); Funding acquisition, S.Z.; Investigation, S.G.; Methodology, S.G., X.G. and S.Z.; Project administration, X.G. and S.Z.; Resources, T.W.; Software, S.G.; Supervision, X.G. and S.Z.; Validation, Y.Z. (Ya Zou) and Y.Z. (Yuting Zhou); Writing—original draft, S.G. and X.G.; Writing review & editing, X.G. and S.Z.

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