Effects of Multi-Scale Climate Change on The Distribution of Invasive Insect Populations and The Development of Ecological Services: A Case Study of *Zeugodacus Cucurbitae* (Coquillett)

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Research Article

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Abstract

In order to clarify the effects of multi-scale climate change on the population distribution and ecological service function of *Z.cucurbitae*, this paper analyzed its suitable distribution area *Z.cucurbitae* in a wide scale using the MaxEnt ecological model. *Z.cucurbitae* were exposed under short-term high temperatures of 33°C, 37°C, 41°C and 45°C for 1h, which were set based on recorded high temperatures in the field. The effects of these temperatures on development and reproduction of *Z.cucurbitae* in successive three generations were evaluated. The results showed that under current climatic conditions, the suitable regions of *Z.cucurbitae* included most of South America, southeast North America, sub-Saharan Africa, part of Oceania and southern coastal areas of Asia. Under two carbon emissions scenarios (RCP4.5 and RCP8.5), the suitable area of *Z.cucurbitae* will expand compared to that under current environment and this expansion will generally be northwards. Short-term high temperature was not conducive to the development and reproduction of *Z.cucurbitae*. The F_1 *Z.cucurbitae* exposed under 45°C for 1h stimulated its oviposition, and the offspring can still continue the population. When the offspring were continuously exposed to short-term high temperature until the F_3, they could not oviposit. In the context of climate change, both large-scale and small-scale changes will affect the distribution and population breeding of *Z.cucurbitae*, which will lead to local sudden outbreak or migration disaster. Therefore, a broad-scale distribution analysis of all populations as a whole will result in a narrow ecological niche and may fail to predict the effects of some local small-scale habitat changes.

Introduction

Climate change is one of the key issues of global environmental change. In the face of climate change, species either tolerate or adapt, or migrate or perish (Pecl et al. 2017). The response forms of species also affect ecological service function by way of biodiversity change. With global warming, the occurrence time, intensity and frequency of high temperature and extreme high temperature events are increasing. Climate change affects the distribution and population development of global organisms, and then affects biodiversity (Stefan and Dim 2011; IPCC 2013). Insects, as typical poikilotherm, are extremely sensitive to climate change. Their ontogeny and population development rates are closely related to climate change, making them ideal materials for studying climate change-species- ecological service function (Bale et al. 2002; Du et al. 2007; Chen and Ma 2010; Ma et al. 2016).

Zeugodacus cucurbitae (Coquillett) are important multi-host, widely distributed and harmful invasive pest of fruit and vegetable crops (Dhillon et al. 2005). Climate change has an important impact on the distribution and population development of *Z.cucurbitae* (Coquillett). Current studies mostly focus on the effects of small-scale and long-term climate conditions on the population development of *Z.cucurbitae* (Coquillett) (Yuan et al. 2005; Li et al. 2008; Wei et al. 2011). On the large-scale context, climate change affects the distribution pattern of pests. On the small-scale, pests usually respond to changes in environmental conditions such as niche temperature rather than long-term constant conditions, and pests can produce responses different from the traditional long-term constant conditions (Ma et al. 2016). Several studies have shown that short-term high temperature had special effects on insects.. For example, exposure of *Sitobion avenae* (Fabricius) to 45°C for 40s, did not result in its mortality (Yang 2013). Exposure of *Ophraella Communa* to short-term high temperature treatment stimulated oviposition, but egg hatching rate decreased (Zhou et al. 2011; Chen et al. 2018). The copulation and oviposition of *Z.cucurbitae* (Coquillett) were stimulated after being treated at 45°C for 1h (Zhou 2016).

Under the background of global climate change, insects can adjust and mitigate the impact of small-scale climate change through phenotypic adaptation and rapid evolutionary response, and thus affect their ecological service function (Bale et al. 2002). Understanding the plasticity of insects and their ability to regulate their own temperature is critical to developing strategies for the conservation of ecological services function (Van et al. 2019). Climate temperature change has the greatest impact on insect growth, development and reproduction, among which high temperature is one of the most important environmental factors as it affects the growth, development and reproduction of insects including *Z.cucurbitae* (Coquillett). For example, short-term high temperature on a small scale can stimulate *Z.cucurbitae* (Coquillett) to produce “toxic excitatory effect” (Zhou 2016). “Toxic excitatory effect” is a special heat response strategy produced by pests under appropriate heat intensity, and it is also considered as a survival strategy against heat stress (short-term or long-term variable heat) (Villalpando et al. 2008; Zhang et al. 2013; Ma et al. 2016). Contemporary adults of *Z.cucurbitae* (Coquillett) increased their spawning quantity after being exposed to short-term high temperature for 1h, thus maintaining population development (Zhou 2016). Additionally, these effects can also be experienced by insect offspring through maternal transmission (Hoffmann and Sgrò 2011). Most studies have focused on the effects of high temperature on *Z.cucurbitae* (Coquillett) (Jiang 2005; Yuan et al. 2005; Zhou 2016; Zeng et al. 2018; Gu et al. 2020). However, the effects of high temperature on the growth, development and survival of successive generations of *Z.cucurbitae* (Coquillett) in small-scale habitats *Z.cucurbitae* (Coquillett) also need to be known. In the context of climate change, the large- and small-scale effects of climate change on *Z.cucurbitae* (Coquillett) need to be studied in combination.

In this study, based on the MaxEnt ecological model, we analyzed the potential suitable distribution range and pattern of *Z.cucurbitae* (Coquillett) under climate change under the current and future climatic conditions using the environmental variable data under three different CO_2 emission concentrations (RCP2.6, RCP4.5 and RCP8.5). The influence of different climatic conditions on its distribution pattern was determined and the trend of invasion and expansion *Z.cucurbitae* (Coquillett) were predicted. In addition, based on the results of studies on the effects of different heat stress on the defense and reproductive strategies of contemporary adult *Z.cucurbitae* (Coquillett), the reproducibility of the “toxic excitatory effect” of short-term high temperature on *Z.cucurbitae* (Coquillett) in different generations was discussed to clarify whether the “maternal effect” appeared.The effects of short-time high temperature in small scale on growth, development and reproduction of *Z.cucurbitae* (Coquillett) in successive generations were evaluated.The results are as follows.

Materials And Methods

Collection of geographical distribution data

The global distribution of *Z.cucurbitae* (Coquillett) was *Z.cucurbitae* (Coquillett) extracted from published data on occurrence. The coordinates of these locations *Z.cucurbitae* (Coquillett) were extracted from the Google map open platform. The data format of sampling points was decimal, and finally a total of 70 *Z.cucurbitae* (Coquillett) distribution points were selected for model construction and prediction of suitable regions.

Acquisition and screening of climate data

Data on 19 environmental factors were used in this study and were obtained from the WordClim database (https: // www. wordclim.org) (Table 1). The data was published in 2005 and covers the period 1960–1990. The accuracy of the data was 2.5 arc-minutes. The tangential method in MaxEnt (version 3.4.1) was used to rank the importance of environmental factors. The correlation analysis to determine the important environmental factors were performed in SPSS (version 26.0). Only one representative environmental factor was retained when the absolute value of the correlation between two ecological factors was greater than or equal to 0.8 (Sunil et al. 2014; Rozhnov et al. 2021). Finally, 10 environmental factors were judged as important for the distribution of *Z.cucurbitae* (Coquillett), which were annual mean temperature (Bio1), monthly mean diurnal temperature difference (Bio2), ratio of diurnal temperature difference to annual temperature difference (Bio3), mean temperature in the wettest quarter (Bio8), mean temperature in the warmest quarter (Bio10), precipitation in the wettest month (Bio13), precipitation in the driest month (Bio14), seasonal variation coefficient of precipitation (Bio15), precipitation in the warmest quarter (Bio18) and precipitation in the coldest season (Bio19). These environmental data were used to predict the suitable regions for *Z.cucurbitae* (Coquillett) under three greenhouse gas emission scenarios (RCP2.6, RCP4.5 and RCP8.5) in a future climate condition *Z.cucurbitae* (Coquillett) (2041–2060). The future climate data used in the study is from the 2050s (2041–2060). The climate variable data are taken from three of the four GHG emission scenarios (RCP2.6, RCP4.5 and RCP8.5) under the Common Climate Model (CCSM4) proposed in the IPPC-AR5 Fifth Assessment Report.Their distribution represents three scenarios of low, medium and high greenhouse gas emissions (He et al. 2020).

Table 1
Climate and environment variables

Variables	Climatic factors
Bio1	Annual average temperature
Bio2	Monthly mean temperature difference between day and night
Bio3	Ratio of diurnal temperature difference to annual temperature difference
Bio4	Seasonal variance of temperature
Bio5	Maximum temperature in the warmest month
Bio6	Lowest temperature in the coldest month
Bio7	Annual variation range of temperature
Bio8	Average temperature in the wettest quarter
Bio9	Average temperature in the driest quarter
Bio10	Average temperature of the warmest quarter
Bio11	Average temperature in the coldest quarter
Bio12	Average annual precipitation
Bio13	Precipitation in the wettest month
Bio14	Precipitation in the driest month
Bio15	Seasonal variation coefficient of precipitation
Bio16	Precipitation in the wettest quarter
Bio17	Precipitation in the driest quarter
Bio18	Precipitation in the warmest quarter
Bio19	Precipitation in the coldest quarter

Model construction and evaluation

Based on the location data and the above 10 important environmental factors screened by MaxEnt, three sets of future climate and environmental data were imported for prediction, and the prediction results were visualized in ArcMap. After beautifying the figure, the prediction map of the suitable area of *Z.cucurbitae* (Coquillett) was derived. In this study, the area under the receiver operating characteristic curve (AUC) was used as an index to measure the accuracy of model prediction (Jorge 2016). A range of 0.5-1, 0.5 corresponded to a completely random prediction; 0.5–0.7 indicate, a poor accuracy of the prediction result; 0.7–0.9 indicate, a moderate accuracy of the prediction result; > 0.9 indicat, a very high accuracy of the prediction result. A proportion of 75% of the coordinate data was randomly selected as the training set of the experiment, and the remaining 25% of the coordinate data was used as the test set.

ROC curve was drawn and AUC value was calculated as the standard to test the accuracy of the prediction results of the model.

Evaluation of the effects of temperature changes in small-scale habitats on the population development of Z.cucurbitae **(Coquillett)**

Pest source for testing and pest management

The insects for this study were collected from balsam pear fields (109°29 'e, 19°30' N) in Nada Town, Danzhou City, Hainan Province, China. Larvae were then fed on artificial diet in the laboratory for breeding. The formula for the diet included 1000g of pumpkin. 1000g of corn flour, 200g of yeast powder, 200g of sucrose, 6g of sodium benzoate, 8ml of concentrated hydrochloric acid and 1000ml of water. Adults were fed on a diet made up of sucrose and yeast powder (W:W) in equal proportion. The average indoor temperature was 25 ± 1°C, 70 ± 5% RH, 14 L:10 days, and a stable laboratory temperature sensitive population was established. In this study, the short-time high temperature treatment insects were all newly emerged adults of *Z.cucurbitae* (Coquillett).

Test reagents and materials

The reagents used in this study, such as yeast powder, corn meal, sodium benzoate, concentrated hydrochloric acid and sucrose, were all purchased from Hainan Qingfeng Biotechnology Co., LTD., and the pumpkins were purchased from the surrounding farmers' markets.

Setting of short-term high temperature treatment for niche

The optimum temperature for *Z.cucurbitae* (Coquillett) was 25–30°C (Wei et al., 2011). External temperatures > 30°C, were considered as high temperature range. The newly emerged adults of the F_1-F_3 generations of *Z.cucurbitae* (Coquillett) were exposed under 25°C (CK), 33°C, 37°C, 41°C and 45°C independently for 1 hr in an artificial climate chamber.

Effects of short-term high temperature on oviposition ability and egg development of Z.cucurbitae **(Coquillett) in successive generations**

Twelve males and females of newly emerged adults from each generation were released together in cages, which was supplied with water and artificial diet for adults and pumpkin flakes for laying eggs. At the end of the exposure to the high temperature treatments, the total spawning quantity (grain), spawning quantity per female (grain), daily spawning quantity per female (grain), pre-spawning period (D), spawning days (D) and egg hatching rate (%) were observed and recorded every day. Each cage of the 12 pairs was considered as 1 replicate and 6 replicates were set up for under each treatment.

Effects of short-term high temperature on the survival and development of successive generations of Z.cucurbitae **(Coquillett)**

The survival rate (%) and longevity (d) of adults in each group and each generation were recorded after the end of short-term high temperature treatment. The survival rate and overall longevity were counted separately from males and females. 12 pairs were divided into 1 replicate with 6 replicates in each group.The larvae of each generation were randomly selected and divided into 6 groups with 120 larvae in each group and 1 replicate in each group. Pupation rate (%), pupa weight (g), eclosion rate (%) and sex ratio were observed and recorded.

Statistical analysis of data

Descriptive statistics and analysis of the data were performed with Excel 2013 and SPSS 20.0 respectively. The recorded indices were: oviposition per female (grain): total oviposition/12, oviposition per female per day (grain): oviposition per female/oviposition period; pre-spawning (d): total time of spawning /12; spawning days (d): spawning period /12; egg hatching rate (%): number of eggs hatched/total number of eggs laid ×100 ;survival rate (%): number of viable insects /12×100; life span (d): total survival time /12, in which the survival rate and total life span were counted separately for male and female; pupation rate (%): pupation number /120×100; eclosion rate (%): eclosion number/total pupa number ×100; sex ratio: female/male.

Results

Analysis of the suitability of Z.cucurbitae **(Coquillett) under broad-scale climate change**

Evaluation results of suitability analysis model

The model evaluation results showed that the AUC values of each prediction results were above 0.96 (Table 2), indicating a high accuracy of the prediction results (Li et al. 2012; Wang et al. 2019). In order to further verify the accuracy of the model, 50 of the location data were randomly selected to be used as the modeling data points for the MaxEnt model. The remaining 20 were used for model evaluation *Z.cucurbitae* (Coquillett). The results of the model evaluation showed that 50 location points including the 20 used as test data fitted the appropriate area of the *Z.cucurbitae* (Coquillett). This further proved the accuracy of the prediction results of the model.

Table 2
Area under the receiver operating characteristic curve

AUC	Current	RCP2.6	2050s RCP4.5	RCP8.5
Training data	0.966	0.967	0.964	0.968
Testing data	0.960	0.964	0.965	0.961

Analysis of suitable regions of Z.cucurbitae **(Coquillett) under current climatic conditions**

Based on the results of the MaxEnt model mentioned above, we analyzed the suitable regions of *Z.cucurbitae* (Coquillett) under current climatic conditions. The results showed that the most suitable areas for the development of *Z.cucurbitae* (Coquillett) were the tropical and subtropical regions, *Z.cucurbitae* (Coquillett) except extremely arid and hot desert areas such as the Sahara. Most of South America, southeastern Parts of North America, sub-Saharan Africa, parts of Oceania, and southern coastal areas of Asia all have favorable climatic conditions for the *Z.cucurbitae* (Coquillett) (Fig. 1). Among them, the medium and high suitable areas *Z.cucurbitae* (Coquillett) were concentrated in southern China, Myanmar, Thailand, India, Vietnam, northeast Pakistan, Japan, South Korea, Indonesia, northern Australia, eastern Tanzania, Cuba, eastern Mexico and southeastern coastal areas of the United States.

Prediction of future suitability zones of Z.cucurbitae (Coquillett) based on climate change with three different carbon emissions

Three different carbon emission scenarios (RCP2.6, RCP4.5 and RCP8.5) were used to predict the suitability zones *Z.cucurbitae* (Coquillett) for *Z.cucurbitae* (Coquillett) worldwide. By 2050 and under RCP2.6, future conditions will be stable, which will produce a relatively stable habitat range for *Z.cucurbitae* (Coquillett) (Fig. 2A). However, under RCP4.5 (Fig. 2B) and RCP8.5 (Fig. 2C), the total area of the suitable area of *Z.cucurbitae* (Coquillett) will increase, compared to current environment and the expansion of this suitable area *Z.cucurbitae* (Coquillett) will be northwards. For example, under RCP4.5 and RCP8.5, Jilin and Heilongjiang provinces in China changed from unsuitable areas to low-suitability areas. Also, suitable areas for the survival of *Z.cucurbitae* (Coquillett) appeared in the southeastern coastal areas of Russia. In addition, low suitability zones for *Z.cucurbitae* (Coquillett) were also located in northern Iran, Iraq and southern Turkey. We speculate that *Z.cucurbitae* (Coquillett) will pose serious threats in most areas of the tropical, subtropical and warm regions of the world in future climate conditions, and even areas around the Mediterranean may become more hospitable to *Z.cucurbitae* (Coquillett) populations.

Effects of short-term high temperature in small-scale habitat on growth, development and reproduction of Z.cucurbitae (Coquillett)

Effects of short-term high temperature on oviposition and egg development of Z.cucurbitae (Coquillett)(F_1 generation)

The effects of short-time high temperature on oviposition and egg development of *Z.cucurbitae* (Coquillett) (F_1 generation) are shown in Table 3. The total spawning quantity decreased with increase in temperature. However, the total spawning quantity, daily spawning quantity and single female spawning quantity increased at 45°C for 1 h, which were 8411 eggs, 91 eggs and 701 eggs, respectively. These were the highest among all treatments, and showed significant difference with CK_1. The early stage of oviposition was shortened with increase in temperature. The shortest stage of oviposition at 45°C was only 6 days, and CK_1 was 11.2 days. The number of spawning days decreased gradually with increase in temperature. It was 92.7 days at 45°C and 159.8 days at CK_1. The hatchability of eggs decreased with increase in temperature. The lowest of 31.9 % was recorded at 45°C and 90.6 % at CK_1.

Table 3
Effects of short term high temperature on oviposition and egg development of *Z.cucurbitae* (Coquillett) (F_1 generation)

Dispose Index	Total amount of spawning	Spawning a quantity	Number of eggs per female	Lay eggs early	Spawning days	Egg hatchability
33°C -1h	7227 ± 42.3c	57 ± 1.6bc	602 ± 3.5c	10 ± 0.3ab	128.2 ± 4.3b	81.5 ± 0.0052b
37°C -1h	6735 ± 50.7d	57 ± 2.4b	561 ± 4.2d	9 ± 0.3bc	118.7 ± 5.5bc	75.7 ± 0.0059c
41°C -1h	6582 ± 49.6d	60 ± 1.9b	548 ± 4.1d	8.7 ± 0.3c	109.5 ± 3.0cd	52.6 ± 0.0024d
45°C -1h	8411 ± 43.1a	91 ± 1.6a	701 ± 3.6a	6 ± 0.3d	92.7 ± 2.6dc	31.9 ± 0.0038e
CK_1	7766 ± 44.1b	49 ± 2.4c	647 ± 3.7b	11.2 ± 0.3a	159.8 ± 5.2a	90.6 ± 0.0026a

Note: Data were mean ± SE. The data in the same column followed by different lowercase letters indicated significant difference at the level of 0.05 (Duncan's new complex range method). The same bellow.

Effects of short-time high temperature on oviposition and egg development of Z.cucurbitae **(Coquillett) (F_2 generation)**

The effects of short-time high temperature on oviposition and egg development of *Z.cucurbitae* (Coquillett) (F_2 generation) are shown in Table 4. The total oviposition, daily oviposition and single female oviposition decreased with increase in temperature. the lowest values of 471 eggs, 17 eggs and 39 eggs, respectively, were recorded under a temperature of 45°C for 1 h, which was significantly different from that obtained under CK_2. The results showed that short-term high temperature treatment for two generations had a negative influence on oviposition. The early stage of oviposition was still shortened with increase in temperature, and the shortest value of 7.2 days was recorded at 45°C while that recorded under CK_2 was 11 days. *Z.cucurbitae* (Coquillett) This high temperature may have promoted the rapid maturation and discharge of eggs, so as to maintain the stability of the population and also to avoid the harm that may be caused by this high temperature. The spawning days also showed a gradual decrease with increase in temperature, and the minimum value of 30 days was recorded at 45°C, and 152.3 days at CK_2., the hatchability of eggs also decreased continuously with increase in temperature. The lowest value of 13.6% was recorded at 45°C, and 91.3% at CK_2. It indicated that increase in temperature resulted in a shorter duration for egg laying but a decrease in the hatchability of eggs.

Table 4
Effects of short term high temperature on oviposition and egg development of *Z. cucurbitae* (Coquillett) (F_2 generation)

Dispose Index	Total amount of spawning	Spawning a quantity	Number of eggs per female	Lay eggs early	Spawning days	Egg hatchability
33°C -1h	6140 ± 35.9b	50 ± 1a	512 ± 3b	10.2 ± 0.3ab	124 ± 2.9b	67.6 ± 0.0049b
37°C -1h	5391 ± 33.1c	49 ± 1.8a	449 ± 2.8c	9.3 ± 0.3b	110.5 ± 3.9c	51 ± 0.0048c
41°C -1h	3324 ± 35.3d	38 ± 0.6b	277 ± 2.9d	8.8 ± 0.4b	88.5 ± 1.9d	33.9 ± 0.007d
45°C -1h	471 ± 11e	17 ± 1.6c	39 ± 0.9e	7.2 ± 0.4c	30 ± 3.2e	13.6 ± 0.0031e
CK_2	7744 ± 30.2a	51 ± 1.5a	645 ± 2.5a	11 ± 0.4a	152.3 ± 3.9a	91.3 ± 0.0037a

Effects of short-term high temperature on oviposition and egg development of Z.cucurbitae **(Coquillett) (F_3 generation)**

The effects of short-time high temperature on oviposition and egg development of *Z.cucurbitae* (Coquillett) (F_3 generation) are shown in Table 5. The total oviposition, daily oviposition and single female oviposition all decreased with increase in temperature. No eggs were laid under exposure to temperature of 45°C for 1h,, which was significantly different from CK_3. This indicated that the oviposition was negatively affected by exposure to multiple short-term high temperatures. The prophase of oviposition lengthened with increase in temperature and the longest period of 14.2 days was recorded at 41°C, and 10.8 days at CK_3. This indicated that three consecutive three generations of short-time high temperature treatments were not beneficial for the development of eggs. The number of spawning days decreased gradually with increase in temperature, and the shortest day 69.3 days was recorded at 41°C and 155 days at CK_3. The hatchability of eggs decreased with increase temperature. It was only 21% at 41°C and 90.7% at CK_3.

Table 5
Effects of short term high temperature on oviposition and egg development of *Z. cucurbitae* (Coquillett) (F_3 generation)

Dispose Index	Total amount of spawning	Spawning a quantity	Number of eggs per female	Lay eggs early	Spawning days	Egg hatchability
33°C -1h	6075 ± 34.2b	50 ± 1a	506 ± 2.8b	11.3 ± 0.2bc	121.2 ± 2.1b	59.7 ± 0.0048b
37°C -1h	2171 ± 40c	21 ± 1b	181 ± 3.3c	12.5 ± 0.3b	105.7 ± 3.8b	41.5 ± 0.0081c
41°C -1h	997 ± 25d	15 ± 0.9c	83 ± 2.1d	14.2 ± 0.4a	69.3 ± 4.4c	21 ± 0.0073d
45°C -1h	0 ± 0e	0 ± 0d	0 ± 0e	0 ± 0d	0 ± 0d	0 ± 0e
CK_3	7780 ± 33.1a	51 ± 2.0a	648 ± 2.8a	10.8 ± 0.3c	155 ± 6.1a	90.7 ± 0.0055a

Effects of short-time high temperature on the survival and development of Z.cucurbitae **(Coquillett) (F_1 generation)**

The effects of short-time high temperature on the survival and development of *Z.cucurbitae* (Coquillett) (F_1 generation) are shown in Table 6. The survival rate decreased with increase in temperature. The survival rate of females in the same treatment was slightly higher than that of males. The survival rate of females in the 33°C treatment was the highest (94.4%), and that of males in the 45°C treatment was the lowest (45.8%), indicating that females were more resistant to high temperature than males. The lifespan shortened with increase in temperature. The longevity of females was longer than that of males in the same treatment. The longevity of females in the 33°C treatment was the longest (150d), and that of males in the 45°C treatment was the shortest (106d), both of which were significantly lower than that of the control.

Table 6
Effects of short term high temperature on survival and development of *Z. cucurbitae* (Coquillett) (F_1 generation)

Index Dispose		Lifespan	Survival rate
33°C-1h	□	150 ± 3.6bc	94.4 ± 0.02ab
	□	144 ± 2.8cd	91.7 ± 0.02b
37°C 1h	□	141 ± 5.9cd	90.3 ± 0.01b
	□	136 ± 5.4cd	87.5 ± 0.02bc
41°C -1h	□	132 ± 3.8cde	80.6 ± 0.02cd
	□	127 ± 4.7de	77.8 ± 0.02d
45°C -1h	□	113 ± 2.9ef	54.2 ± 0.02e
	□	106 ± 1.5f	45.8 ± 0.03f
CK_1	□	180 ± 5.4a	100 ± 0a
	□	167 ± 3.6ab	100 ± 0a

Effects of short-term high temperature on the survival and development of Z.cucurbitae **(Coquillett) (F_2 generation)**

The effects of short-time high temperature on the survival and development of *Z.cucurbitae* (Coquillett) (F_2 generation) are shown in Table 7. The survival rate decreased with the increase in temperature. The survival rate of females in the same treatment was slightly higher than that of males. The highest survival rate of females in the 33°C treatment was 88.9%, and the lowest survival rate of males in the 45°C treatment was 33.3%, indicating that females were still more heat-resistant than males in the second high temperature treatment. But the survival rate was lower than that in the F_1 generation. The longevity decreased with increase in temperature and was lower than that of the F_1 generation. The longevity of females was longer than that of males in the same treatment. The longevity of females in the 33°C treatment was the longest (145d), and that of males in the 45°C treatment was the shortest (49d), both of which were significantly lower than that of the control. Pupa weight, pupation rate and emergence rate decreased with increase in temperature, and the lowest values recorded were 0.0067g, 17.5% and 37.5% respectively at 45°C, which were significantly lower than those of the control. The sex ratio increased with increase in temperature, and the maximum of 6:1 was recorded at 45°C, indicating that females were still more heat-resistant than males, which was consistent with the above mentioned survival rate and longevity of females compared with males.

Table 7
Effects of short term high temperature on survival and development of *Z. cucurbitae* (Coquillett) (F_2 generation)

Index Dispose		Lifespan	Survival rate	Pupae weight	Pupation rate	Emergence rate	Sex ratio
33°C-1h	□	145 ± 2.7b	88.9 ± 0.02b	0.0162 ± 0.0002b	82.5 ± 0.011b	86.0 ± 0.024b	1.43:1
	□	139 ± 3.5bc	86.1 ± 0.02b				
37°C-1h	□	132 ± 4.0bc	68.1 ± 0.03c	0.0136 ± 0.0002c	76.7 ± 0.010c	60.9 ± 0.014c	1.55:1
	□	126 ± 4.5cd	61.1 ± 0.02cd				
41°C-1h	□	110 ± 1.7de	58.3 ± 0.02d	0.0103 ± 0.0002d	45 ± 0.018d	51.7 ±0.022c	1.8:1
	□	108 ± 1.6e	54.2 ± 0.02d				
45°C-1h	□	51 ± 3.3f	36.1 ± 0.02e	0.0067 ± 0.0008e	17.5 ± 0.011e	37.5 ± 0.042d	6:1
	□	49 ± 3.3f	33.3 ± 0.03e				
CK_2	□	173 ± 3.6a	100 ± 0a	0.0248 ± 0.0001a	93.3 ± 0.011a	98.2 ± 0.011a	1.12:1
	□	170 ± 3.8a	100 ± 0a				

Effects of short-time high temperature on the survival and development of Z.cucurbitae **(Coquillett) (F_3 generation)**

The effects of short-time high temperature on the survival and development of *Z.cucurbitae* (Coquillett) (F_3 generation) are shown in Table 7. Pupa weight, pupation rate and emergence rate decreased with increase in temperature, and the lowest values recorded were 0.0037g, 8.3% and 13.9% respectively at 45°C, which were significantly lower than those of the control. The sex ratio increased with increase in temperature, and the maximum of 3:1 was recorded at 41°C. All the females emerged at 45°C, indicating that the females were more heat-resistant than the males. The survival rate decreased with increase in temperature. The survival rate of females in the same treatment was slightly higher than that of males. The highest survival rate of females (63.9%) was recorded under 33°C and the lowest was under 45°C. All of them died after high-temperature treatment, indicating that females were still more heat-resistant than males after multiple high-temperature treatments. However, the survival rate was lower than that of F_1 and F_2 generations. The longevity decreased with increase in temperature and was lower than that of the F_1 and F_2 generations in general. The longevity of females in the same treatment was longer than that of males. The longevity of females in the 33°C treatment was the longest (141 days), and that in 45°C treatment was the shortest (0 days), which were significantly lower than those in the control.

Table 8
Effects of short term high temperature on survival and development of *Z. cucurbitae* (Coquillett) (F_3 generation)

Index Dispose		Lifespan	Survival rate	Pupae weight	Pupation rate	Emergence rate	Sex ratio
33°C-1h	□	141 ± 1.6b	63.9 ± 0.02b	0.0156 ± 0.0002b	61.7 ± 0.011b	43.3 ± 0.017b	1.46:1
	□	138 ± 1.4bc	59.7 ± 0.01bc				
37°C-1h	□	127 ± 3.8cd	54.2 ± 0.02cd	0.0094 ± 0.0003c	40.8 ± 0.008c	35.0 ± 0.026b	1.83:1
	□	122 ± 4.0d	52.8 ± 0.02de				
41°C-1h	□	90.2 ± 3.6d	47.2 ± 0.02ef	0.0049 ± 0.0006d	18.3 ± 0.011d	18.1 ±0.059c	3:1
	□	88.7 ± 3.5d	43.1 ± 0.01f				
45°C-1h	□	0 ± 0e	0 ± 0g	0.0037 ± 0.0003d	8.3 ± 0.0516e	13.9 ± 0.090d	1:0
	□	0 ± 0e	0 ± 0g				
CK_3	□	183 ± 3.5a	100 ± 0a	0.0256 ± 0.0001a	94.2 ± 0.015a	97.3 ± 0.012a	1.2:1
	□	178 ± 3.4a	100 ± 0a				

Discussion

A variety of ecological models have been applied to study insect adaptation on a wide scale. Due to the different ecological theories and algorithms used for the models, the prediction results are different. For example, Kong et al. (2008) used CLIMEX and DIVA-GIS to predict and analyze the suitable areas of *Z.cucurbitae* (Coquillett), and the results showed that the whole of Australia was suitable for *Z.cucurbitae* (Coquillett). However, our results showed that only the northern part of Australia showed low suitability for *Z.cucurbitae* (Coquillett), Other areas were not suitable for the survival of *Z.cucurbitae* (Coquillett). The central and western regions of Australia are desert areas, and the high temperature and drought are not suitable for their survival *Z.cucurbitae* (Coquillett). This result proves that the prediction accuracy of the model used in this study was better than that obtained with the CLIMEX model. In addition, the research model used in our study requires the distribution data of species, and data on environmental variables which can be downloaded from the official website of WordClim. Therefore, the model can also be applied for the prediction of suitable areas for other species.

The impact of climate change on population development can be linear or non-linear (Grünig et al. 2020). When the response to the impact is not linear, the rate of change of population development is usually faster than that of linear change (Dakos et al. 2019). Large scale climate and niche conditions jointly affect the population development of *Z.cucurbitae* (Coquillett). Under These conditions may influence *Z.cucurbitae* (Coquillett) to suddenly erupt in areas that they did not occur previously. More seriously, other insects with similar climatic conditions to *Z.cucurbitae* (Coquillett) are likely to invade this area, thus aggravating the harm (Brockerhoff and Liebhold 2017). Therefore, in the context of global climate change, in addition to the impact of large-scale climate change on the development of insects and other biological populations, attention should also be paid to the outbreak of insect migration caused by niche climate change, especially in their non-occurring areas.

The growth, development, survival and reproduction of insects are regulated by temperature, it develops at different rates over different temperature ranges (Culos and Tyson 2014). The duration and frequency of high temperature in niche are important characteristics of heat effect (Ma et al. 2018; Zhu et al. 2019). Rapid temperature increase usually enhances insect metabolism and produces offspring, which enables rapid population development (Atkinson 1994; Cara et al. 2018; Tseng et al. 2019). In this study, it was found that after short-time high temperature treatment in small-scale habitat, the prophase of oviposition of *Z.cucurbitae* (Coquillett) adults in F_1 and F_2 generations was shortened with increase in temperature. Zhou (2016) observed the anatomy of the ovaries of the *Z.cucurbitae* (Coquillett) after high temperature treatment, and confirmed that high temperature accelerated ovarian development and promoted oviposition *Z.cucurbitae* (Coquillett). When the number of high temperature treatments increased, the oviposition behavior of *Z.cucurbitae* (Coquillett) was inhibited, and the prophase of their oviposition *Z.cucurbitae* (Coquillett) in the F_3 generation was prolonged. Gu et al. (2020) showed that the prophase of oviposition of *Z.cucurbitae* (Coquillett) was prolonged with increase in temperature after 34–42°C (12 h) stress, which was consistent with the results of this study. High temperature accelerated the growth rate of *Z.cucurbitae* (Coquillett) and shortened their oviposition duration, but it was not conducive to their reproduction. *Z.cucurbitae* (Coquillett) The oviposition of the F_1 generation increased under exposure to 45°C for 1h. However, the total oviposition, daily egg production, single female oviposition and oviposition days of the other treatments were significantly lower than those of the control, and decreased with increase in temperature and treatment times. High temperatures were not conducive for the oviposition of *Z.cucurbitae* (Coquillett) generally. For example, the egg hatchability of the adults of *Ophraella communai* was decreased when treated at 40°C, 42°C and 44°C for 3 h, compared to the control at 28°C (Chen et al. 2018). After the adults of *Carposina sasakii* was subjected to short-term high temperature stress, the spawning quantity gradually decreased with increase in temperature and treatment time (Li et al. 2014).

High temperatures can disrupt ion balance in insect cells (hyperkalemia), thereby impairing neurophysiological functions and damaging mitochondria (O 'Sullivan et al. 2017; Bowler 2018). They can also destroy the water retaining structure in insects, even if the wax layer and oil in the insect epidermis are liquefied, increase water loss, indirectly cause damage and lead to death due to drying in insects (Gibbs 2002; Chown et al. 2011). The results of this study showed that the survival rate and life span of *Z.cucurbitae* (Coquillett) decreased gradually with increase in temperature from 33°C to 45°C. At the same temperature and with increase in the number of treatments (one treatment per generation), the survival rate and life span of *Z.cucurbitae* (Coquillett) decreased. That of the F_3 generation *Z.cucurbitae* (Coquillett) could not survive after exposure to 45°C for 1 h. He et al. (2019) subjected the adults of *Assara inouei* Yamanaka to short-term high temperature stress, and the results showed that the survival rate of adult gradually decreased and the life span gradually shortened with increase in temperature and treatment time, which is consistent with the results of this study. This indicates that the intensity, duration and frequency of high temperature are closely related to the survival and life span of insects.

The female adults of *Z.cucurbitae* (Coquillett) were more tolerant to short-time high temperature than the male adults as they had a higher survival rate and life span than that of male adults after short-time high temperature. Zhou (2016) conducted short-term high temperature and fluctuating high temperature treatment on the adults of *Z.cucurbitae* (Coquillett). The results showed that the survival rate and longevity of female adults were higher than that of males indicating that they were more heat-resistant than males, which was consistent with the results in this paper. Short-term high temperature treatment also affected the sex ratio (female/male) of the offspring of *Z.cucurbitae* (Coquillett), which increased with increase in temperature. The sex ratio of *Z.cucurbitae* (Coquillett) pupae emergence in the 45°C treatment group of the F_2 generation was the largest, which was 6: 1. Gu et al. (2020) found *Z.cucurbitae* (Coquillett) that after 12 h of high temperature treatment, the female ratio of offspring of *Z.cucurbitae* (Coquillett) adults gradually increased with the increase in treatment temperature. In this study, it was found that when the newly emerged adults of the F_2 generation underwent high temperature treatment, the adults of the offspring *Z.cucurbitae* (Coquillett) which emerged in the 45°C group of the F_3 generation were all female adults with a sex ratio of 1:0. After two successive high temperature treatments, the number of F_3 generation males of *Z.cucurbitae* (Coquillett) decreased or even could not complete emergence.

High temperatures not only affect contemporary adults, but also affect the next generation through "maternal effect". The results of this study showed that short-term high temperature treatment of *Z.cucurbitae* (Coquillett) adults resulted in decreased egg hatching rate, pupation rate and emergence rate of the next generation, increased sex ratio and decreased pupa weight, resulting in smaller offspring. The weight of pupae was also decreased when the larvae of *Spodoptera mauritia* and *Heliothis virescens* experienced continuous heat stress of 35°C (Ghazanfar et al. 2020). Heat damage can induce changes in insect body size, and rapidly increasing temperature usually increases insect metabolism, resulting in increased generation of offspring and rapid population development (Atkinson 1994; Cara et al. 2018; Tseng et al. 2018). Although smaller offspring individuals are more prone to dehydration and overheating (Gardner et al. 2011), small individuals may promote the absorption of water and nutrients by the insect gut or intestinal symbiotic bacteria to avoid heat damage (Kikuchi et al. 2016). However, there are few studies on insect growth trajectories and their potential physiological mechanisms under continuous short-term high temperature events. Therefore, a more systematic evaluation of the effects of short-time high temperature on the population of *Z.cucurbitae* (Coquillett) needs to be further studied.

When insects are stimulated by certain environmental conditions such as high temperature, they will produce "toxic excitatory effect", which is a special survival coping strategy of temperature adaptation. It is also considered a survival strategy against high temperature stress (Villalpando et al. 2008; Zhang et al. 2013; Ma et al. 2016). In this study, the oviposition of the F_1 generation *Z.cucurbitae* (Coquillett) exposed to 45°C for 1h was significantly higher than that of the control. A similar phenomenon was also observed for *Bactocera dorsalis* (Hendel). The oviposition of female *B. dorsalis* (Hendel) exposed to 35°C for 2 h showed a decrease compared to that of the control (25°C), while oviposition of that exposed under 40°C for 2 h was 1445.4 eggs / d, which was significantly higher than that of the control (691.89 eggs / d) (Ren et al. 2010). Zhou (2016) found that the frequency of copulation and oviposition of *Z.cucurbitae* (Coquillett) increased after exposure to 45°C for 1h, but the "toxic excitatory effect" *Z.cucurbitae* (Coquillett) was unstable, and was no longer effective when the treatment duration was prolonged. The results of our study showed that there was no increase in oviposition after the F_2 and F_3 generations were subjected to 45°C for 1 h, and the "toxic excitatory effect" was difficult to reproduce between different generations. This indicate that "toxic excitatory effect" was not only affected by the duration of high temperature treatment, but also by the number of high temperature treatments. This proved again that the "toxic excitatory effect" was unstable. Therefore, the intensity, duration and frequency of high temperature in the field should be fully considered in the control of *Z.cucurbitae* (Coquillett) during the high temperature season. Also, these characteristics of short-term high temperatures can also be used for the control of *Z.cucurbitae* (Coquillett).

The distribution of species is also affected by its own dispersal capacity, human factors, geographical barriers, and interactions among species. The normal development of *Z.cucurbitae* (Coquillett) is not only affected by temperature, but also restricted by environmental factors such as humidity and rainfall (Li et al. 2016; He et al. 2019). In this study, precipitation in the wettest month (bio13), precipitation in the driest month (bio14), annual mean temperature (bio1), monthly mean diurnal temperature difference (bio2) and precipitation in the warmest season (bio18) were the most influential environmental factors to the suitable area of *Z.cucurbitae* (Coquillett). The results indicated that temperature and humidity were important to their normal growth and development *Z.cucurbitae* (Coquillett). For example, Egypt, Syria and other places are located near 30° north latitude, and the temperature conditions in these areas can meet the growth and development of *Z.cucurbitae* (Coquillett). Under normal circumstances, these areas can be suitable for *Z.cucurbitae* (Coquillett). However, due to the dry climate and low annual precipitation in these areas, *Z.cucurbitae* (Coquillett) cannot survive here. In this study, the effects of niche temperature on the population development of *Z.cucurbitae* (Coquillett) were analyzed. The effects of other environmental factors on thire population development *Z.cucurbitae* (Coquillett) can be further studied.

Declarations

Author Contributions

YYL, AQW, BZ, SHP and SHZ participated in the study design and analysis the manuscript. HMY and JLL, participated in study design and helped to draft the manuscript. Supervision and financially support, SHZ, Revised and processed. All authors read and approved the final manuscript.

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Figures

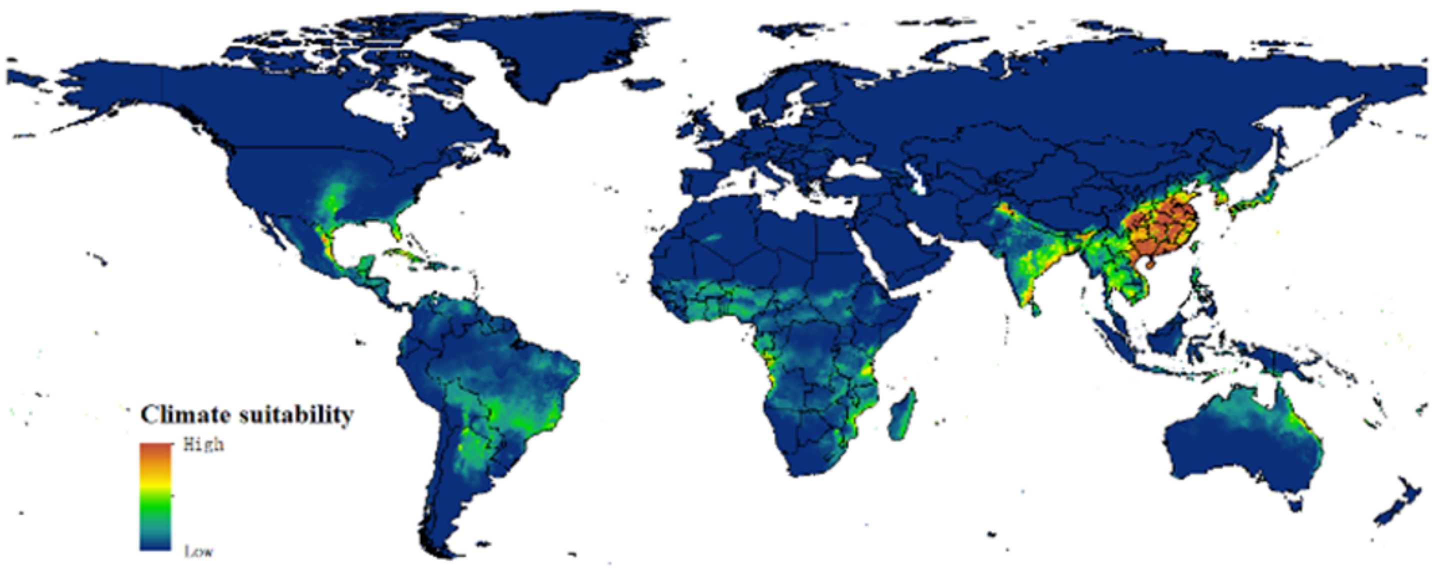

Figure 1

Potential distribution of Z. cucurbitae (Coquillett) worldwide under current climatic conditions

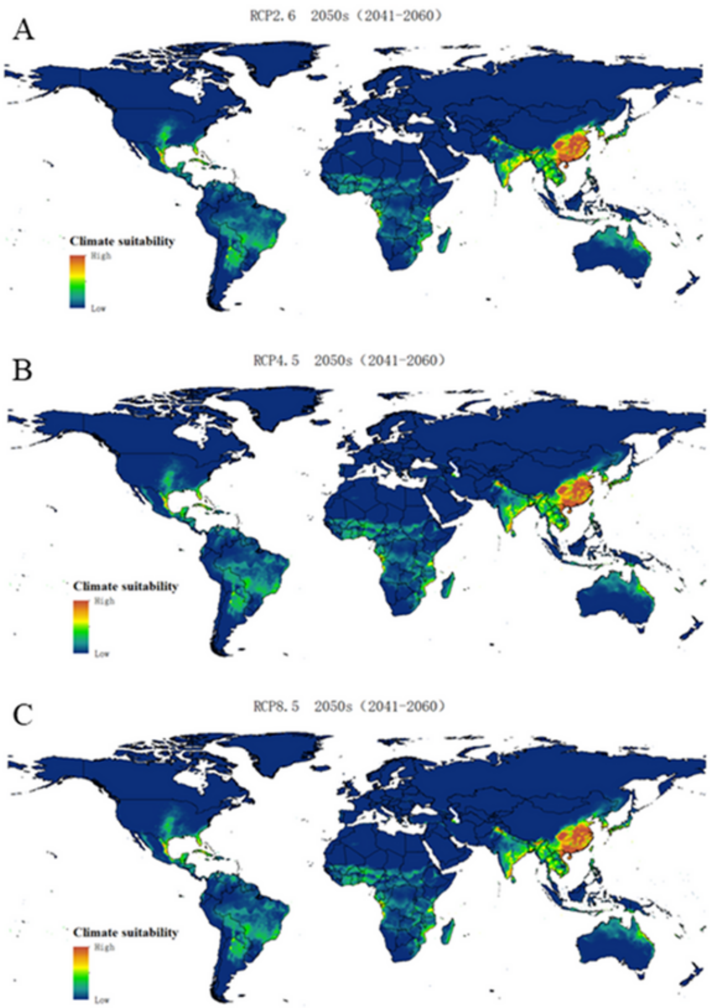

Figure 2

Distribution of Z.cucurbitae (Coquillett) in the global suitable area under climate conditions in 2050. (A. Suitable areas under RCP2.6;B. Suitable areas under RCP4.5;C. Suitable areas under RCP8.5)