



# Protected agriculture matters: Year-round persistence of *Tuta absoluta* in China where it should not

Xiao-xian Liu<sup>1</sup>, Minglu Yang<sup>2</sup>, Judit Arnó<sup>3</sup>, Darren J. Kriticos<sup>4,5</sup>, Nicolas Desneux<sup>6</sup>, Myron P. Zalucki<sup>1,5</sup>, and Zhaozhi Lu<sup>1,\*</sup>

<sup>1</sup> Shandong Engineering Research Center for Environment-Friendly Agricultural Pest Management, College of Plant Health and Medicine, Qingdao Agricultural University, Qingdao 266109, China.

<sup>2</sup> Agriculture College of Tarim University, Alar 843300, China.

<sup>3</sup> IRTA, Sustainable Plant Protection Program, 08348 Cabrils, Institute of Agrifood Research and Technology, Barcelona, Spain.

<sup>4</sup> Cervantes Agritech Pty Limited, 7 Plummer Street, Weetangera, ACT 2614, Australia.

<sup>5</sup> School of Biological Sciences, The University of Queensland, Brisbane, QLD 4072, Australia.

<sup>6</sup> Université Côte d'Azur, INRAE, UMR ISA, 06000 Nice, France

\* Corresponding author: zhaozhi\_lv@sina.com, zhaozhi@ms.xjb.ac.cn

With 3 figures

**Abstract:** *Tuta absoluta* (Lepidoptera: Gelechiidae) originates from the South American tropics but has become a major invasive pest of tomato and other Solanaceae crops worldwide. Agricultural protected facilities (APFs) such as greenhouses and plastic tunnels may provide thermal conditions that allow the survival of *T. absoluta* in temperate zones with cold winters. In this study, a CLIMEX model was used to investigate the dual effects of increasing use of APFs and climate warming on the potential distribution and seasonal dynamics of *T. absoluta* in China. Our model showed that the northern boundary for year-round population persistence in China, ignoring APFs, was approximately 30°N, covering about 21% of China's area suitable under current climate. The modelled suitable area increased to 31% and northern boundary for year-round population persistence shifted to 40°N in 2080 under global warming. When APF refuges are included, the potential suitable area was 78% under the current climate and 79% under global warming. This suggests that, in the future, the increasing use of APFs will increase the areas at risk of *T. absoluta* invasion significantly more than global warming because APFs effectively protect *T. absoluta* from harsh northern winters. In addition, vegetable production in surrounding open fields will be at risk of invasion during milder seasons when APFs are opened and *T. absoluta* can disperse. Therefore, the micro-climate of APFs should be considered as part of the invasion process, and Integrated Pest Management should be simultaneously implemented inside and outside APFs for the rational management *T. absoluta*.

**Keywords:** agricultural protected facility; biological invasion; climate warming; greenhouse; plastic tunnel

## 1 Introduction

The spread of invasive species is facilitated by socioeconomic and political factors associated with globalization (Bertelsmeier et al. 2017) including trade and tourism, changed agricultural practices, and changing social trends (Seebens 2019). In addition, global warming enables invaders to spread to previously unsuitable climatic zones (Warren et al. 2018; McNitt et al. 2019; Ma et al. 2021). Increasing temperature has direct and indirect effects on population dynamics of insects, notably invasive ones (Dangles et al. 2008; Wang et al. 2021; Wang and Ma 2022).

The effect of temperature heterogeneity within a landscape, as opposed to the average ambient temperature, on

the ecology of invasive pests has received little attention (Heller & Gordon 2006), largely because surrounding spatial microclimates cannot be measured at public meteorological stations (Faye et al. 2017; Formby et al. 2018). The thermal buffering provided by sheltered habitats such as natural geological formations (aspect and orientation) and by artificial structures such as Agriculture Protected Facilities (APFs) within a landscape can ameliorate temperature extremes and may promote the survival of insects, especially for tropical and subtropical species invading temperate and frigid zones (Formby et al. 2018).

The use of APFs such as greenhouses and plastic tunnels in a farming landscape is likely to buffer extreme thermal events allowing insect survival and development in

winter (Wang et al. 2015). In China, the area of APFs has increased from 50,000 ha in 1995 to 5.6 million ha in 2019 (Department of Agricultural Mechanization Management 2021). This dramatic increase may be a major factor promoting the northwards spread of pests such as whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) and the invasive leaf miner *Liriomyza sativae* Blanchard (Diptera: Agromyzidae) which cannot survive in open fields in temperate areas in winter (Wang et al. 2015). Such facilities may become hotspots for the persistence and population increase of invasive species originating from tropical or sub-tropical areas (Wang et al. 2015) and may be a source of pests dispersing into open fields when conditions outside APFs are more favorable.

The tomato leaf miner *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is native to South America but has successfully colonized most continents in the last two decades (Desneux et al. 2011; Campos et al. 2017; Biondi et al. 2018), threatening local production and the export of solanaceous crops to pest-free countries (Desneux et al. 2010; Han et al. 2019; Mansour et al. 2018; Desneux et al. 2022). There are two patterns of infestation by *T. absoluta*: year-round population persistence that occurs mainly in tropical and sub-tropical areas, and a transient population that occurs mainly in temperate zones where this pest cannot overwinter in open fields (van Damme et al. 2015; Han et al. 2018; McNitt et al. 2019; Campos et al. 2021b). APFs may promote the geographical expansion of this invasive species into otherwise unsuitable areas such as northern Europe and northern China (Han et al. 2019; Zhang et al. 2021) and facilitate a switching from ephemeral to permanent populations. Despite this understanding, the refuge role of APFs in facilitating pest invasion and colonization has not been sufficiently considered within pest risk assessment (PRA), integrated pest management (IPM), or biosecurity policy (though note van Damme et al. 2015).

Various studies have investigated pest distributions using CLIMEX an ecological niche model (ENM). The fitted CLIMEX model describes the species growth and stress responses to climatic variables and applies these response functions to the climate at each location on a daily/weekly basis. The reliance upon distribution data in CLIMEX is tempered by the requirement that the fitted model parameters are biologically reasonable and agree with what is known of the species biology, including phenology (Webber et al. 2011; Kriticos et al. 2015). Large areas of APFs when used as reference sites may affect the calibration of models giving misleading estimates of potential distributions, especially in open field landscapes.

Previous bioclimatic models for *T. absoluta* were based on occurrence records from published papers and reports, GBIF and CABI (Desneux et al. 2010; Santana et al. 2019; Han et al. 2019). These distribution records do not clearly differentiate open fields or greenhouses and resulting models may be misconstrued, as the occurrences in glasshouses do

not reflect the species response to the local prevailing climate. This suggests that some parameters in previous models may need to be revisited after clarifying the known distribution of *T. absoluta* in natural or open field landscapes (van Damme et al. 2015; Martins et al. 2016), and by extension the potential distribution.

In our study, the role of APFs and climate change were used to assess the invasion of pest species of tropical origin into China, using *T. absoluta* as a model species. The following questions were addressed: (1), currently and in the future, where is the geographical boundary of successful overwintering by *T. absoluta* in open fields without the thermal refuge of APFs? (2), how do global warming and APFs work together to affect the potential distribution of *T. absoluta*? and (3), how do APFs help to bridge populations of *T. absoluta* inside and outside the APFs at a local scale? The answer to these questions will help us to understand how tropical and subtropical pests can invade a landscape with APFs under current climatic conditions and under global warming and will inform biosecurity policy for APF management in China.

## 2 Material and methods

### 2.1 Simulating the geographical distribution of *Tuta absoluta*

#### 2.1.1 The known sites of *Tuta absoluta*

Occurrence records for *T. absoluta* were obtained from the Global Biodiversity Information Facility (GBIF); first occurrence and outbreak records were from the Center for Agriculture and Bioscience International (CABI) and the European and Mediterranean Plant Protection Organization (EPPO) supplemented with records from published literature (Santana et al. 2019). These occurrence records were divided into two categories: (1) areas of natural overwintering for the species, and (2) areas of non-natural (refuge) overwintering. Based on the biology of *T. absoluta*, sites with an ambient average daily temperature below 5 °C for more than 21 days were considered as non-natural overwintering sites (van Damme et al. 2015; Campos et al. 2021a; 2021b). Of 711 recorded occurrences, 493 were from natural overwintering sites and 218 were from non-natural overwintering sites (see supplementary Fig. 1).

#### 2.1.2 CLIMEX model

We used CLIMEX (Hearne Scientific Software, version 4.02, Australia, Kriticos et al. 2015) to model the climate suitability patterns for *T. absoluta*. The “Compare Location (one species)” module was employed for estimating the potential distribution of *T. absoluta*. The Ecoclimatic Index (EI), which ranges from 0 to 100, is used to describe the overall climatic suitability of a given location for a species to persist. An EI value of 100 represents ideal conditions for

survival, whereas an EI value of 0 indicates unsuitable conditions for survival. The EI value is determined by the annual growth index ( $GI_A$ ) and the stress index (SI):

$$EI = GI * SI \quad (1)$$

Each of the indices used to calculate annual growth and stress are based on functions that describe the species positive or negative response to temperature and moisture estimated from either laboratory experiments or from fitting the species distribution or fitting to phenology data (Zalucki & Van Klinken 2006).

SI is determined by the cold stress (CS), heat stress (HS), dry stress (DS), and wet stress (WS) according to the following equation (2) and each stressor is calculated weekly (Kriticos et al. 2015):

$$SI = (1 - CS/100) * (1 - HS/100) * (1 - DS/100) * (1 - WS/100) \quad (2)$$

$GI_A$  is the product of a temperature (TI) and moisture index (MI), calculated weekly and summed over the year (Equation 3):

$$GI_A = \sum TI * MI \quad (3)$$

### 2.1.3 Climatic data and scenarios

To build the model, we used year-round occurrence data for *T. absoluta* populations in open fields in South America (Supplementary Fig. 1) to estimate parameters (Supplementary Table 1); Mediterranean data was used for model validation (Supplementary Fig. 1b). The CliMond CM30\_1995H\_V2 climatic dataset interpolated at 30 arc minute (~50 km) resolution was used (Kriticos et al. 2015). This dataset has long-term monthly climate means centered on the year 1995 for precipitation, maximum temperature, minimum temperature, and relative humidity at 9:00 and 15:00 hours.

Future climate scenarios were extracted from the Climate futures databases (CliMond) for twenty-year averages centered on 2080. The CMIP5 Global Climate Data were derived using the Representative Carbon Pathways (RCP) emission scenarios (Kriticos et al. 2012). Recognizing the substantial and irreducible uncertainties in the future greenhouse gas emissions scenarios, we used the RCP8.5 emission scenario to stress-test modelled systems with a plausible but extreme scenario, so that emerging threats could be identified clearly. This scenario is equivalent to SSP585, or a business-as-usual emissions projection (Zhu et al. 2020).

### 2.1.4 Fitting parameters

Parameters were calibrated using the natural overwintering data to eliminate inaccurate predictions because of data from APFs (Supplementary Fig. 1). The agreement between the species distribution and the model for seasonal phenol-

ogy provided cross-validation for our model (Kriticos et al. 2015). The following assumption was made about the conditions under which the pest could exist in a rainfed environment and an irrigated crop environment: for the irrigation scenario, CLIMEX rainfall data were modified with top-up irrigation of 1.5 mm day<sup>-1</sup> and 0.5 mm day<sup>-1</sup> in summer and winter respectively, which encompasses the range of soil moisture for crops growing optimally (Kriticos et al. 2015). The detailed parameters of modeling on *T. absoluta* are presented in supplementary Table 1.

## 2.2 The effect of APFs on *Tuta absoluta* distribution

### 2.2.1 The use of APFs for vegetable production in China

Tomato, eggplant, and sweet pepper are often cultivated in APFs in winter (plastic tunnels are more than 90% of APFs, Supplementary Fig. 4). These solanaceous crops are suitable hosts for *T. absoluta* (Desneux et al. 2010; Sylla et al. 2019; Rostami et al. 2020). We used the percentage of APFs used to grow all vegetables to adjust cold stress in the CLIMEX model (details in 2.2.2). The mean annual area of APFs (unit: 10<sup>3</sup> hectares) from 2008-2018 in each province in China (except Taiwan, Hongkong and Macao) was obtained from the Greenhouse Data Sharing Platform (Department of Agricultural Mechanization Management 2021) and Chinese Statistics Yearbook (National Bureau of Statistics 2019). To predict the percentage of APFs in total vegetable crops in 2080, we extrapolated a linear regression model fitted to the above yearly data using SPSS software (IBM SPSS Statistics 20). The utilization rate of APFs was described by: % of APFs = 0.0061\*year-12.216; R<sup>2</sup> = 0.732, P < 0.01. Except for Yunnan, Guizhou, Guangxi, Hunan, Jiangxi and Hainan, the other provinces in China had a significant increase in use of APFs such as plastic tunnels (Supplementary Fig. 4).

### 2.2.2 Modelling the potential distribution of *Tuta absoluta*

Firstly, we calculated the area of APF (including the greenhouse, glasshouse, and plastic tunnels) divided by the area of vegetable cultivation in each province in China, expressed as a percentage. According to Natural Breaks (Jenks), the calculated results were divided into six categories and assigned a new metric (PI) with the following values (0, 0.2, 0.4, 0.6, 0.8 and 1). Then we multiplied PI by the CS values in the CLIMEX model to calculate a new CS (NCS) and new SI (NSI) value using equations 4 and 5 below. The NCS value was substituted into equation (2) and equation (1) to generate a new EI (NEI) for *T. absoluta* using equation (6). This NEI was considered a measure of the role of APFs in mediating habitat conditions for *T. absoluta* in winter (see details in Supplementary Fig. 1). The adjustments to CS and EI were done on CLIMEX output in ArcGIS (Environmental Systems Research Institute, Inc. Version 10.2). The PI values, that represent the possibility that the moth could find APFs as a shelter in cold winter, were linked to the shape

file for each province in ArcGIS. We converted the shapefile with PI values into a grid map with the same resolution using “feature into raster” tools in ArcGIS. The PI grid map was multiplied by the original CS grid map to get a new CS and EI grid map using the raster calculator in ArcGIS.

$$\text{NCS} = (1 - \text{PI}) * \text{CS} \quad (4)$$

$$\text{NSI} = (1 - \text{NCS}/100) * (1 - \text{HS}/100) * (1 - \text{DS}/100) * (1 - \text{WS}/100) \quad (5)$$

$$\text{NEI} = \text{GI} * \text{NCS} \quad (6)$$

In general, an EI of more than 30 represents a favorable climate for a species (Kriticos et al. 2015). The EI values were divided into four categories: Not suitable (EI = 0), Low suitability (0 < EI < 10), Moderate suitability (10 < EI < 30), High suitability (EI > 30). The CLIMEX model was validated qualitatively by evaluating its ability to estimate climate suitability for currently known occurrences of *T. absoluta* in geographic regions not used for parameter fitting (Supplementary Fig. 1b). EI values > 0 were taken to mean that the insect pest could potentially invade and persist in this area.

## 2.3 The effect of APFs on the population dynamics and dispersal of *Tuta absoluta* with climate change

### 2.3.1 Survival and phenology

Firstly, spatial temperature variation was considered at a large geographic scale. The EI was simulated under four scenarios: C1, current climate without APFs; C2, current climate with APFs as refuges; F1, future climate (2080) without APFs; and F2, future climate with APFs. The climate data was sourced from CliMond, APF data from government statistics (Department of Agricultural Mechanization Management 2021), and our predictions based on current vegetable production (see 2.2.1 and Supplementary Fig. 4).

Secondly, thermal buffering within APFs was considered with respect to the phenology and survival of this insect pest in winter. The GI<sub>w</sub> (weekly Growth Index) was used to describe the phenology of the *T. absoluta* population under the four different scenarios (C1, C2, F1 and F2) described above in 16 sites which are major tomato producers in China. Four scenarios of increasing temperature within APFs were devised based on ambient temperatures in open fields and the thermal requirements of vegetable production in APFs in winter: increased by 5°C (where the average temperature in January in open fields is above 5°C), increased by 10°C (where the average temperature in January in open fields is between -5°C and 5°C), increased by 15°C (where the average temperature in January in open fields is between -15°C and -5°C) and increased by 20°C (where the average temperature in January in open fields is below -15°C). Temperature data was from sensors in different sites and published works from colleagues from these regions (Chen & Kang 2005).

### 2.3.2 Dispersal

APFs not only offer refuges for insect pests to overwinter, but also provide foci for re-invasion when ambient temperatures outside increase in spring. The Buffer function in ArcGIS (Environmental Systems Research Institute, Inc. Version 10.2) was used to estimate the dispersal range of *T. absoluta* when APFs were opened in spring. The buffer points of different densities were used to simulate the effect of APFs at different percentages of the total vegetable-growing area. We selected 0.2 km, 0.5 km, 1 km, 1.5 km, 2 km, 3 km, 4 km, and 5 km as a buffer radius to estimate the dispersal range in spring in a non-natural overwintering area (Supplementary Fig. 5) based on the reported dispersal which is generally less than 1km (see Supplementary Table 2).

## 3 Results

### 3.1 Validation of the model and biological parameters

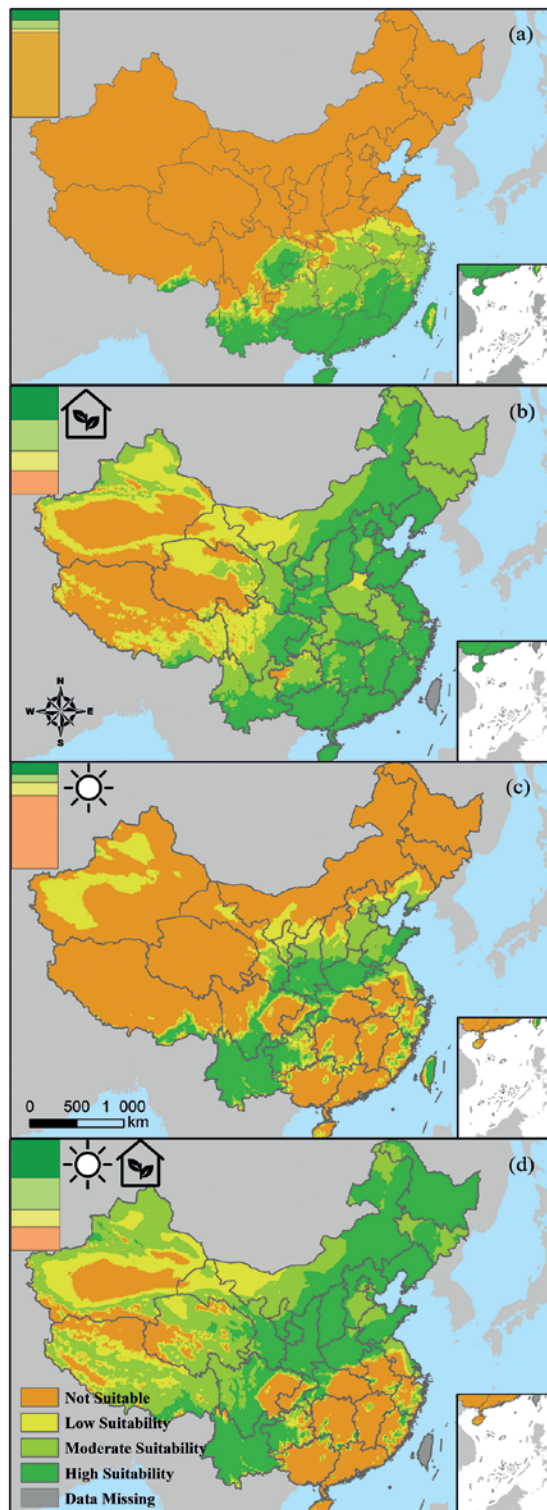
Our model with modified parameters (Supplementary Table 1) produced a distribution which was consistent with the current distribution of the moth in South America and the Mediterranean region (Supplementary Fig. 1). Our simulated results were consistent with 97% of occurrence records for these two regions and Sub-Saharan Africa. This confirmed that our model was accurate for describing the distribution of *T. absoluta*.

### 3.2 The effect of climate warming and APFs on the distribution of *Tuta absoluta*

Under the current climate and without APFs (scenario C1), our model simulated the northern boundary of year-round *T. absoluta* populations at approximately 30°N, making the subtropical and tropical zones of China south of 30°N the most suitable for persistence of this pest (Fig. 1a). This area equates to about 21% of the total area of China.

Under the 2080 C2 scenario of global warming, the northern boundary of year-round *T. absoluta* populations shifts to approximately 40°N, and some subtropical and tropical regions in eastern China become less suitable for persistence of this pest (Fig. 1c). The total suitable area for the moth in China increases to approximately 31% of the total area occupied, though suitability declines in southern and southwest China (Fig. 1c). Parts of the northwestern region and northeastern China become somewhat suitable for *T. absoluta* due to increased temperatures in winter and early spring (Fig. 1c).

The use of APFs has a significant effect on climate suitability patterns for *T. absoluta* distribution under the current climate and future global scenarios. With APFs as refuges, the area potentially suitable for year-round infestation is approximately 77.9% of the total area under the current climate (F<sub>1</sub> scenario, Fig. 1b). Under the dual influence of APFs and climate warming in the future (F<sub>2</sub> scenario), the potential



**Fig. 1.** The Ecoclimatic Index (EI) for *Tuta absoluta* modelled using CLIMEX: (a), under current climatic conditions and no APFs (Scenario C1); (b), under current climatic conditions and with APF as refuges (Scenario F1); (c), for 2080 under global warming and no APFs (Scenario C2) and (d), for 2080 under global warming and with APFs as refuges (Scenario F2). The stacked column chart in top left corner of each map represents the percentage of area in each suitability category.

distribution of *T. absoluta* increases by only 0.9% to 78.8% of the total area (Fig. 1d).

### 3.3 The change in population dynamics of *Tuta absoluta*

APFs provide refuge habitats over the winter enabling populations of *T. absoluta* to persist year-round, such as Sites 1, 2, 3 and 4 (Fig. 2). In Shouguang, Shandong (Site 5) and Kashgar, Xinjiang (Site 10), the pest survives the winter because of the effective refuge role of APFs at those sites, albeit with a low GIw. The time when GIw is equal to zero is shortened from 6 months to 2 months in Chifeng, Inner Mongolia (Site 14 and 15) and NingAn, Heilongjiang (Site 16); all these sites (14–16) are characterized by a long, freezing winter (Fig. 2).

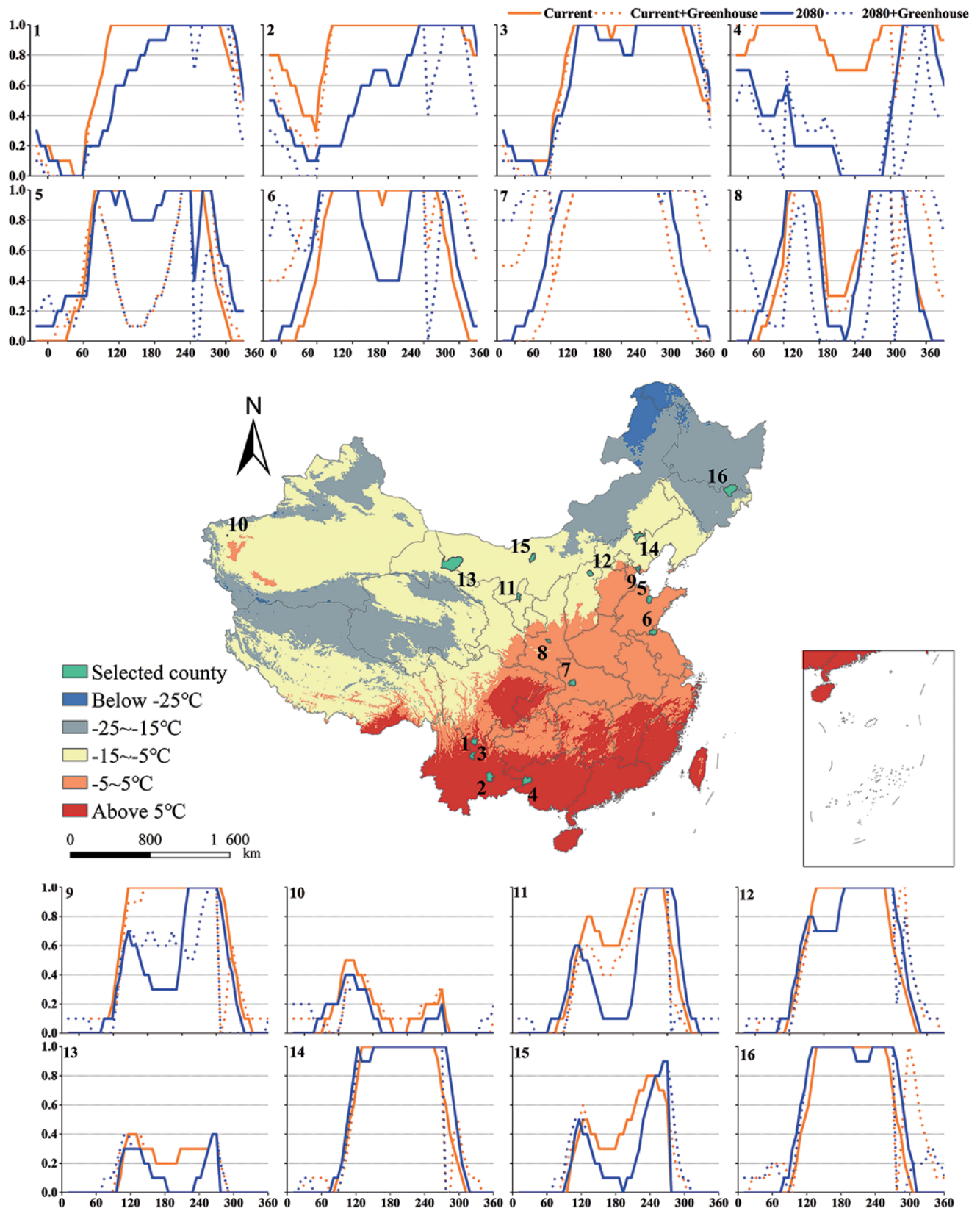
### 3.4 The dispersal of *Tuta absoluta* from APFs to surrounding open fields

In spring, when APFs such as plastic tunnels are opened, *T. absoluta* may disperse from these thermal refuges to surrounding fields (Supplementary Fig. 5). The relationship between the percentage of area covered by *T. absoluta* ( $Z$ ), the dispersal distance of *T. absoluta* in km ( $X$ ), and the use of APFs ( $Y$ ), measured as the protected area per 3200 km<sup>2</sup> (the average area of a county in China), was described well by the nonlinear surface ( $R^2 = 0.932$ ,  $P < 0.001$ ) (Fig. 3). The area at risk of pest infestation outside APFs is affected by both the dispersal distance and APF use. When dispersal distance ( $X$ ) is more than 2 km, the area infested surrounding the APF increases rapidly (Fig. 3 and Supplementary Fig. 5).

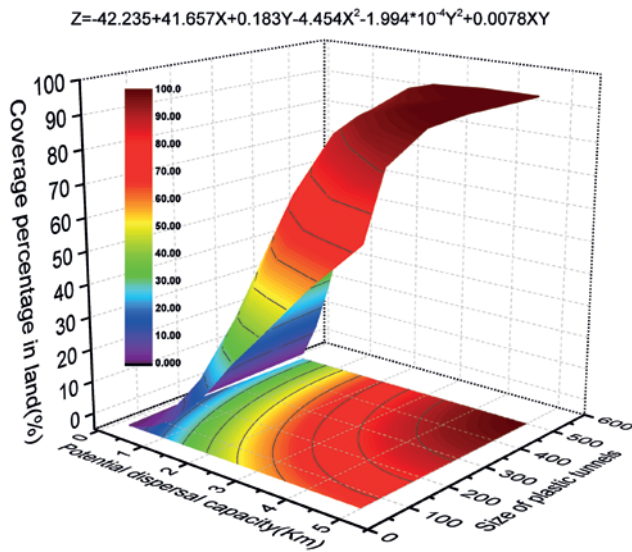
## 4 Discussion

This is the first report of APFs increasing the distribution range of *T. absoluta* northwards in China beyond our previous estimate of approximately 30°N. *Tuta absoluta* cannot persist unaided through the long cold winter in temperate zones (Desneux et al. 2010; Martins et al. 2016). Our model demonstrates how the presence of APFs can increase the ability of *T. absoluta* to survive the harsh winters in northern China because APFs offer thermal buffering and prolong the pest's development window in seasons that are not naturally suitable (Fig. 1 and 2). Moreover, the refuge role of APFs facilitates *T. absoluta* switching from winter host plants within APFs to spring-summer hosts in open fields, resulting in the year-round persistence (Fig. 2).

APFs have a much greater effect on increasing the area suitable for *T. absoluta* than a global warming scenario regardless of the interaction between APFs and global warming. Surprisingly, our model suggests that global warming will have little effect on the suitable area for *T. absoluta* (around 1% increasing) if APFs are present (Fig. 1b, 1d), despite including a 10% increase in the absence of APF (Fig. 1a, 1c). Nonetheless, the size of suitable areas for *T.*



**Fig. 2.** (a) The location of selected counties in China (green) used for modelling *Tuta absoluta* phenology. Different colors indicate different temperature zones. The temperature data was obtained from WorldClim. (b) The change of Growth Index (GI) at each site over the whole year under the current climate (solid orange line), future climate at 2080 (solid blue line), current climate and agriculture protection facilities (APFs) (dotted orange line), and 2080 climate and APFs (dotted blue line).



**Fig. 3.** The relationship between the percentage of area potentially covered by dispersing *Tuta absoluta*, (Z), the potential dispersal distance of this pest, (X), and APF use measured as the protected area within a region of 3200 km<sup>2</sup> (the average area of all counties in China).

*absoluta* affected by APFs were significantly increased both in the current climate and future global warming scenarios, respectively (Fig. 1c, 1d). With or without the shelter of APFs in China, global warming will likely shift the suitable area for *T. absoluta* northwards, but it also significantly decreases the suitable area in the subtropics and tropics which is in accordance to what has been previously reported for many other species (FAO 2008, see <http://www.fao.org/3/a-ai785e.pdf>).

APFs in temperate regions enable *T. absoluta*, as well as other tropical insects, to persist through harsh winters becoming point-sources for serial re-invasion of open fields in spring when local climatic conditions improve. How quickly such patchy populations spread will depend on the size of source populations, the local cropping landscape, and the species dispersal abilities (Fig. 3, Supplementary Fig. 5). In this case, *T. absoluta* would move from APFs to the surrounding open fields where suitable hosts are available in spring and summer. Later in autumn, populations can move back into APFs when host plants are replanted and re-established within the APFs. This spatial switch is key to explaining why subtropical and tropical pests can successfully invade colder areas and establish year-round populations in temperate or sub-frigid zones worldwide, such as Tajikistan, Kazakhstan, Kyrgyzstan, Uzbekistan and Russia (EPPO 2021).

Our simulation of the distribution and phenology of *T. absoluta* is based on an ENM (Ecological niche model) to describe the species response to climate. A correlative SDM (species distribution model) would likely fit the occurrence

data very well but be precisely wrong if the occurrences in areas with harsh winters are taken at face value. As two recent examples for *Bemisia tabaci* show, when using SDMs, it is not even sufficient to filter records on the basis that they have been observed in the field (Ramos et al. 2018). In these cases, field records from extremely cold regions (adjacent to APFs) were included in the model training data, and consequently the potential for establishment in cold environments was significantly overestimated.

The known distribution of *T. absoluta* is still limited in China (Zhang et al. 2021). To slow the further spread of this invasive pest in China, it is necessary to strengthen the management campaign on the frontline inside and outside APFs. Where *T. absoluta* has established, tailored IPM programs, such as seedlings free of pest infestation, adjusting the sowing date of solanaceous hosts, rotation with non-host crops in the open fields surrounding APFs and insect-proof screens would help mitigate pest infestation and help to better control *T. absoluta* in China as well as in other tomato producing countries in temperate zones.

**Acknowledgements:** This work was supported by National Key R&D program of China (2021YFD1400200). CERCA Program / Generalitat de Catalunya provided funding to JA, and ND was funded in part by the Horizon Europe project ADOPT-IPM (n°101060430).

## References

- Bertelsmeier, C., Ollier, S., Liebhold, A. & Keller, L. (2017). Recent human history governs global ant invasion dynamics. *Nature Ecology & Evolution*, 1(7), 0184. <https://doi.org/10.1038/s41559-017-0184>.
- Biondi, A., Guedes, R. N. C., Wan, F. H., & Desneux, N. (2018). Ecology, worldwide spread, and management of the invasive South American tomato pinworm, *Tuta absoluta*: Past, present, and future. *Annual Review of Entomology*, 63(1), 239–258. <https://doi.org/10.1146/annurev-ento-031616-034933>
- Campos, M. R., Biondi, A., Adiga, A., Guedes, R. N. C., & Desneux, N. (2017). From the Western Palaearctic region to beyond: *Tuta absoluta* 10 years after invading Europe. *Journal of Pest Science*, 90(3), 787–796. <https://doi.org/10.1007/s10340-017-0867-7>
- Campos, M. R., Amiens-Desneux, E., Béarez, P., Soares, M. A., Ponti, L., Biondi, A., ... Desneux, N. (2021a). Impact of low temperature and host plant on *Tuta absoluta*. *Entomologia Experimentalis et Applicata*, 169(11), 984–996. <https://doi.org/10.1111/eea.13094>
- Campos, M. R., Béarez, P., Amiens-Desneux, E., Ponti, L., Gutierrez, A. P., Biondi, A., & Desneux, N. (2021b). Thermal biology of *Tuta absoluta*: Demographic parameters and facultative diapause. *Journal of Pest Science*, 94(3), 829–842. <https://doi.org/10.1007/s10340-020-01286-8>
- Chen, B., & Kang, L. (2005). Implication of pupal cold tolerance for the northern over-wintering range limit of the

- leafminer *Liriomyza sativae* (Diptera: Agromyzidae) in China. *Applied Entomology and Zoology*, 40(3), 437–446. <https://doi.org/10.1303/aez.2005.437>
- Dangles, O., Carpio, C., Barragan, A. R., Zeddani, J. L., & Silvain, J. F. (2008). Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. *Ecological Applications*, 18(7), 1795–1809. <https://doi.org/10.1890/07-1638.1>
- Department of Agricultural Mechanization Management. (2021). Ministry of Agriculture and Rural Affairs of the People's Republic of China. <http://data.sheshiyuanyi.com/AreaData/>
- Desneux, N., Han, P., Mansour, R., Arnó, J., Brévault, T., Campos, M. R., ... Biondi, A. (2022). Integrated pest management of *Tuta absoluta*: Practical implementations across different world regions. *Journal of Pest Science*, 95, 17–39. <https://doi.org/10.1007/s10340-021-01442-8>
- Desneux, N., Luna, M. G., Guillemaud, T., & Urbaneja, A. (2011). The invasive South American tomato pinworm, *Tuta absoluta*, continues to spread in Afro-Eurasia and beyond: The new threat to tomato world production. *Journal of Pest Science*, 84(4), 403–408. <https://doi.org/10.1007/s10340-011-0398-6>
- Desneux, N., Wajnberg, E., Wyckhuys, K. A. G., Burgio, G., Arpaia, S., Narváez-Vasquez, C. A., ... Urbaneja, A. (2010). Biological invasion of European tomato crops by *Tuta absoluta*: Ecology, geographic expansion and prospects for biological control. *Journal of Pest Science*, 83(3), 197–215. <https://doi.org/10.1007/s10340-010-0321-6>
- EPPO (2021). EPPO Global Database: *Tuta absoluta* (Meyrick). <https://gd.eppo.int/taxon/GNORAB>
- Faye, E., Rebaudo, F., Carpio, C., Herrera, M., & Dangles, O. (2017). Does heterogeneity in crop canopy microclimates matter for pests? Evidence from aerial high-resolution thermography. *Agriculture, Ecosystems & Environment*, 246, 124–133. <https://doi.org/10.1016/j.agee.2017.05.027>
- Formby, J. P., Rodgers, J. C., III, Koch, F. H., Krishnan, N., Duerr, D. A., & Riggins, J. J. (2018). Cold tolerance and invasive potential of the redbay ambrosia beetle (*Xyleborus glabratus*) in the eastern United States. *Biological Invasions*, 20(4), 995–1007. <https://doi.org/10.1007/s10530-017-1606-y>
- GBIF: The Global Biodiversity Information Facility (2022). What is GBIF? Available from <https://www.gbif.org/what-is-gbif>
- Han, P., Bayram, Y., Shaltiel-Harpaz, L., Sohrabi, F., Saji, A., Esenali, U. T., ... Desneux, N. (2019). *Tuta absoluta* continues to disperse in Asia: Damage, ongoing management and future challenges. *Journal of Pest Science*, 92(4), 1317–1327. <https://doi.org/10.1007/s10340-018-1062-1>
- Han, P., Zhang, Y. N., Lu, Z. Z., Wang, S., Biondi, A., ... Desneux, N. (2018). Are we ready for the invasion of *Tuta absoluta*? Unanswered key questions for elaborating an Integrated Pest Management package in Xinjiang, China. *Entomologia Generalis*, 38(2), 113–125. <https://doi.org/10.1127/entomologia/2018/0739>
- Heller, N. E., & Gordon, D. M. (2006). Seasonal spatial dynamics and causes of nest movement in colonies of the invasive Argentine ant (*Linepithema humile*). *Ecological Entomology*, 31(5), 499–510. <https://doi.org/10.1111/j.1365-2311.2006.00806.x>
- Kriticos, D., Maywald, G., Yonow, T., Zurcher, E., Herrmann, N. & Sutherst, R. (2015). *CLIMEX. Version 4. Exploring the Effects of Climate on Plants, Animals and Diseases*.
- Kriticos, D. J., Webber, B. L., Leriche, A., Ota, N., Macadam, I., Bathols, J., & Scott, J. K. (2012). CliMond: Global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution*, 3(1), 53–64. <https://doi.org/10.1111/j.2041-210X.2011.00134.x>
- Ma, C. S., Zhang, W., Peng, Y., Zhao, F., Chang, X. Q., Xing, K., ... Rudolf, V. H. W. (2021). Climate warming promotes pesticide resistance through expanding overwintering range of a global pest. *Nature Communications*, 12(1), 5351. <https://doi.org/10.1038/s41467-021-25505-7>
- Mansour, R., Brévault, T., Chailleux, A., Cherif, A., Grissa-Lebdi, K., Haddi, K., ... Biondi, A. (2018). Occurrence, biology, natural enemies and management of *Tuta absoluta* in Africa. *Entomologia Generalis*, 38(2), 83–112. <https://doi.org/10.1127/entomologia/2018/0749>
- Martins, J. C., Picanço, M. C., Bacci, L., Guedes, R. N. C., Santana, P. A., Jr., Ferreira, D. O., & Chediak, M. (2016). Life table determination of thermal requirements of the tomato borer *Tuta absoluta*. *Journal of Pest Science*, 89(4), 897–908. <https://doi.org/10.1007/s10340-016-0729-8>
- McNitt, J., Chungback, Y. Y., Mortveit, H., Marathe, M., Campos, M. R., Desneux, N. et al. (2019) Assessing the multi-pathway threat from an invasive agricultural pest: *Tuta absoluta* in Asia. *Proceedings of the Royal Society B*, 286, 1–9 <https://doi.org/10.1098/rspb.2019.1159>
- National Bureau of Statistics. (2019). China statistical yearbook. <http://www.stats.gov.cn/tjsj/ndsj/>
- Ramos, R. S., Kumar, L., Shabani, F., & Picanço, M. C. (2018). Mapping global risk levels of *Bemisia tabaci* in areas of suitability for open field tomato cultivation under current and future climates. *PLoS One*, 13(6), e0198925. <https://doi.org/10.1371/journal.pone.0198925>
- Rostami, E., Madadi, H., Abbasipour, H., Allahyari, H., & Cuthbertson, A. G. S. (2020). Pest density influences on tomato pigment contents: The South American tomato pinworm scenario. *Entomologia Generalis*, 40(2), 195–205. <https://doi.org/10.1127/entomologia/2020/0788>
- Santana, P. A., Jr., Kumar, L., da Silva, R. S., & Picanço, M. C. (2019). Global geographic distribution of *Tuta absoluta* as affected by climate change. *Journal of Pest Science*, 92(4), 1373–1385. <https://doi.org/10.1007/s10340-018-1057-y>
- Seebens, H. (2019). Invasion Ecology: Expanding Trade and the Dispersal of Alien Species. *Current Biology*, 29(4), 120–122. <https://doi.org/10.1016/j.cub.2018.12.047>
- Sylla, S., Brévault, T., Monticelli, L. S., Diarra, K., & Desneux, N. (2019). Geographic variation of host preference by the invasive tomato leaf miner *Tuta absoluta*: Implications for host range expansion. *Journal of Pest Science*, 92(4), 1387–1396. <https://doi.org/10.1007/s10340-019-01094-9>
- van Damme, V., Berkvens, N., Moerkens, R., Berckmoes, E., Wittemans, L., De Vis, R., & de Clercq, P. (2015). Overwintering potential of the invasive leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) as a pest in greenhouse tomato production in Western Europe. *Journal of Pest Science*, 88(3), 533–541. <https://doi.org/10.1007/s10340-014-0636-9>
- Wang, X. J., & Ma, C. S. (2022). Challenge generality of prediction based on Jensen's inequality: Moderate and large temperature fluctuations can lead to opposite performance deviation at high mean temperature. *Entomologia Generalis*, 42(5), 681–689. <https://doi.org/10.1127/entomologia/2022/1410>
- Wang, C., Zhang, X., Pan, X., Li, Z., & Zhu, S. (2015). Greenhouses: Hotspots in the invasive network for alien species. *Biodiversity*



- and Conservation*, 24(7), 1825–1829. <https://doi.org/10.1007/s10531-015-0876-x>
- Wang, Y., Yan, J., Sun, J. R., Shi, W. P., Harwood, J. D., Monticelli, L. S., ... Chen, J. (2021). Effects of field simulated warming on feeding behavior of *Sitobion avenae* (Fabricius) and host defense system. *Entomologia Generalis*, 41(6), 567–578. <https://doi.org/10.1127/entomologia/2021/1271>
- Warren, R., Price, J., Graham, E., Forstenhaeusler, N., & Van DerWal, J. (2018). The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°C rather than 2°C. *Science*, 360(6390), 791–795. <https://doi.org/10.1126/science.aar3646>
- Webber, B. L., Yates, C. J., Le Maitre, D. C., Scott, J. K., Kriticos, D. J., Ota, N., ... Midgley, G. F. (2011). Modelling horses for novel climate courses: Insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models. *Diversity & Distributions*, 17(5), 978–1000. <https://doi.org/10.1111/j.1472-4642.2011.00811.x>
- Zalucki, M., & Van Klinken, R. (2006). Predicting population dynamics of weed biological control agents: Science or gazing into crystal balls? *Australian Journal of Entomology*, 45(4), 331–344. <https://doi.org/10.1111/j.1440-6055.2006.00560.x>
- Zhang, G. F., Xian, X. Q., Zhang, Y. B., Liu, W. X., Liu, H., Feng, X. D., ... Dai, A. M. (2021). Outbreak of the South American tomato leafminer, *Tuta absoluta*, in the Chinese mainland: Geographic and potential host range expansion. *Pest Management Science*, 77(12), 5475–5488. <https://doi.org/10.1002/ps.6588>
- Zhu, H. H., Jiang, Z. H., Li, J., Li, W., Sun, C. X., & Li, L. (2020). Does CMIP6 Inspire More Confidence in Simulating Climate Extremes over China? *Advances in Atmospheric Sciences*, 37(10), 1119–1132. <https://doi.org/10.1007/s00376-020-9289-1>

Manuscript received: 22 August 2022

Revisions requested: 8 October 2022

Modified version received: 25 January 2023

Accepted: 12 April 2023

The pdf version (Adobe JavaScript must be enabled) of this paper includes an electronic supplement: Supplementary Table 1–2, Supplementary Figure 1–5