

# Modelling the potential geographic distribution of *Trissolcus japonicus*: a biological control agent of the brown marmorated stink bug, *Halyomorpha halys*

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**Abstract** *Trissolcus japonicus* Ashmead (Hymenoptera: Scelionidae) is an endoparasitoid of the eggs of the brown marmorated stink bug, *Halyomorpha halys* Stål (Hemiptera: Pentatomidae), a major agricultural pest native to China, Japan, South Korea and Taiwan. We used CLIMEX to estimate the potential global distribution of *T. japonicus* with particular reference to New Zealand. In its native range the model predicts the presence, or a potential expansion, of *T. japonicus* into most of humid-subtropical and humid-continental areas. Globally, the model projects that many temperate, Mediterranean and subtropical areas could suit the establishment of *T. japonicus*. In New Zealand, the north appears moderately to highly suitable for *T. japonicus*,

while southern regions are mostly marginal. The risk posed by *T. japonicus* to non-target species in New Zealand is predicted to vary between different non-targets. CLIMEX projections of the potential distribution of *T. japonicus* provide guidance for release sites of this parasitoid if approved for importation and release in New Zealand.

**Keywords** Bioclimatic model · CLIMEX · Climate matching · Scelionidae · Pentatomidae · Parasitoid

## Introduction

The brown marmorated stink bug, *Halyomorpha halys* Stål (Hemiptera: Pentatomidae), is a temperate/subtropical invasive species native to China, Japan, South Korea and Taiwan (Lee et al. 2013). It has a broad host range of more than 300 plant species (Lee et al. 2013; Bergmann et al. 2016), many of which are of economic importance, especially within the Fabaceae, Rosaceae and Solanaceae, but also including Poaceae, Rutaceae, Vitaceae and Actinidiaceae (Zhang et al. 2000; Yang et al. 2009; Lee et al. 2013; Bergmann et al. 2016). *Halyomorpha halys* has invaded the United States, Canada, and a number of European countries from its Asian homeland, and has become a major pest in some regions and crops (Haye et al. 2015; Leskey and Nielsen 2018). Most recently, in early 2017, *H. halys* was detected for the first time in South America

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in Chile (Faúndez and Rider 2017). In New Zealand, *H. halys* has been repeatedly intercepted at the border and is recognised as a major threat to New Zealand's economy and environment. Biosecurity authorities acknowledge that there is a high risk of establishment in New Zealand as a result of the numerous interceptions and the ability of *H. halys* adults to disperse quickly over long distances (Duthie 2012). A recently published CLIMEX model, which predicts the potential global geographical distribution of *H. halys* (Kriticos et al. 2017), estimates that, in New Zealand, most of the North Island and a number of areas in the northern and eastern sides of the South Island are suitable for the establishment of *H. halys*. If (or when) *H. halys* does establish in New Zealand, then successful biological control by natural enemies could provide a key management tool in concert with specific crop pest management programmes. Effective natural enemies will act in both managed and unmanaged habitats across New Zealand's landscapes.

*Trissolcus japonicus* Ashmead (Hymenoptera: Scelionidae) [syn. *Trissolcus halyomorphae* Yang; Talamas et al. (2013)] is a solitary endoparasitoid of the eggs of *H. halys* in its native range, and like this host, also overwinters as an adult, indicating a close synchrony between the two species (Nystrom Santacruz et al. 2017; Zhang et al. 2017). The minimum threshold temperature for development of *T. japonicus* was estimated to be 12.2 °C, with a thermal constant of 132.5 degree-days (Qiu et al. 2007). These parameters suggest that *T. japonicus* could potentially have up to ten generations per year in Beijing, China (Qiu et al. 2007). Female *T. japonicus* lay 42 eggs on average and prefer to oviposit in eggs no older than 1–3 days (Qiu et al. 2007). Yang et al. (2009) concluded that *T. japonicus* has the characteristics of an excellent biocontrol agent, including a high female-to-male ratio, short developmental time, and many more generations than its host. Yang et al. (2009) also found that *T. japonicus* could successfully parasitize the eggs of a few other species of pentatomid pests in laboratory mass rearings, and they suggested that such alternative hosts may help support high population levels of the parasitoids in China. Zhang et al. (2017) also collected *T. japonicus* from several native Pentatomidae species in China, indicating that the parasitoid is oligophagous within the Pentatomidae in its native range.

When a biological control agent is introduced into a new location, it needs to be able to persist and thrive in the climatic conditions of its new environment (Robertson et al. 2008; van Driesche et al. 2008). Natural enemies obtained from areas with similar climatic conditions to the recipient area are generally more likely to succeed in achieving effective control (Hoelmer and Kirk 2005). Conversely, when climatic mismatch occurs between both the donor and the recipient area, it is frequently considered to be responsible for the failure of establishment, or low effectiveness in controlling the target pest (Hoelmer and Kirk 2005; Dhileepan et al. 2006). As part of a classical biocontrol programme, climatic modelling can help to quantify the similarity of climatic conditions between invaded areas and the native range of the invasive species. Using this information it is possible to find the areas with the best climatic match to search for and collect natural enemies (van Driesche et al. 2008). This method improves the chance of establishment when releasing natural enemies in the recipient country (Hoelmer and Kirk 2005; Dhileepan et al. 2006), thus improving the success of biocontrol programmes (Sutherst 2003). Climate plays an important role in limiting the potential geographical distribution of species (Kriticos et al. 2012), and, as such, climatic variables have been widely used to predict the potential distribution of invasive alien species as part of risk assessments (Saavedra et al. 2015; Kriticos et al. 2017), and also of natural enemies used in biocontrol programmes (Robertson et al. 2008; Olfert et al. 2016).

Niche modelling is often used to estimate areas with suitable climatic conditions for the survival of species (Anderson et al. 2003). A number of bioclimatic modelling software (e.g. CLIMEX, BIOCLIM, DOMAIN) have been widely used in biocontrol (Dhileepan et al. 2006; Olfert et al. 2016) or in pest risk assessment (Baker et al. 2000; Sutherst 2014) to estimate the similarity of climatic conditions between the home range and the receiving range of an invasive species. CLIMEX is a well-recognised climate modelling software that was designed with biological control applications in mind (Kriticos et al. 2015a). It has been widely used to estimate the potential distribution of insect pests (Kriticos et al. 2007; Saavedra et al. 2015), weeds (Potter et al. 2009; Watt et al. 2011), diseases (Yonow et al. 2004; Watt et al. 2009), and natural enemies (Mo et al. 2000; Olfert

et al. 2016). In contrast to many other methods of predicting species distribution, CLIMEX includes a global meteorological database and process-based algorithms, which make it more reliable and accurate than regression-based models when projecting a species' potential distribution into novel climates (Kriticos et al. 2015a). In the present study, data on the developmental biology of *T. japonicus* and records of its current global distribution were used to develop a CLIMEX niche model to estimate the potential global distribution of *T. japonicus*. The model was then used to predict the potential distribution of *T. japonicus* within New Zealand and to assess potential environmental risks by comparison with the known distribution of non-target host species.

## Materials and methods

### Outline of the CLIMEX model

CLIMEX is a dynamic model that integrates the weekly growth responses of a population to climate and calculates a series of weekly and annual indices that allow the potential distribution of a species based on these calculations to be estimated (Kriticos et al. 2015a). Using ecophysiological parameters and meteorological data, CLIMEX uses an annual growth index ( $GI_A$ ) to describe the potential for population growth as a function of soil moisture and temperature during favourable conditions, and up to eight stress indices (heat, cold, wet, dry stresses and their interactions) to simulate the ability of the population to survive unfavourable conditions (Kriticos et al. 2015a). The annual growth index, ( $GI_A$ ), is calculated using:

$$GI_A = \frac{100}{52} \sum_{w=1}^{52} (TI_w \times MI_w)$$

where  $w$  is the week of the year,  $TI_w$  the temperature index for week  $w$ , and  $MI_w$  the moisture index for week  $w$ .

CLIMEX also includes a mechanism for defining the minimum annual developmental heat sum (degree-days above the base temperature for development; PDD) during the growing season that is necessary for individual development and hence population persistence. This parameter is used to calculate the potential number of generations per year and may also act as a limiting condition when a minimum of one generation

needs to be completed for the species to survive in a determined location. To complete a generation, the species must experience the number of growing degree-days set for PDD (Kriticos et al. 2015a). Once the growth and stress indices are calculated weekly, they are combined to generate an overall annual index of climatic suitability, the Ecoclimatic Index (EI). This index provides an overall measure of the climatic suitability of a given location to support a permanent population of the species (Kriticos et al. 2015a). EI is calculated from:

$$EI = GI_A \times SI \times SX$$

where  $GI_A$  is the annual growth index,  $SI$  is the total stress and  $SX$  is the interaction between stresses.

The EI ranges from 0 to 100, with these limits respectively describing unsuitable and optimal conditions for survival of the species. However, maximum values are rare and only occur in highly stable environments, such as those found near the equator (Kriticos et al. 2015a) or those created artificially in incubators (Legaspi and Legaspi 2010). In practice, EI values greater than 20 have been demonstrated to be able to support substantial population densities (Sutherst 2003; Kriticos et al. 2015a). The classification of EI used here was: unsuitable ( $EI < 1$ ), marginal ( $EI = 1-10$ ), moderate ( $EI = 11-15$ ), high ( $EI = 16-25$ ) and optimal suitability ( $EI > 25$ ).

### Location records of *T. japonicus*

Data describing the native distribution of *T. japonicus* were compiled from GPS records available on the Hymenoptera Online database (Cora et al. 2017). Information from the most recent records in the US was retrieved from both the Hymenoptera Online database (Cora et al. 2017) and published papers (Talamas et al. 2015; Jentsch 2016; Milnes et al. 2016; Ferro 2017).

### CLIMEX model parameters and meteorological data

Using the 'Compare Locations' module, parameter values (Table 1) were determined: (i) from experimental data on the thermal requirements of the species, which were obtained from the literature (Li and Liu 2004; Qiu et al. 2007), and by (ii) fitting the projected distribution to known observations of *T.*

**Table 1** CLIMEX parameter values used for modelling the potential distribution of *T. japonicus*

Parameter	Description	Values	Units <sup>a</sup>
Moisture	SM0 = lower soil moisture threshold	0.1	
	SM1 = lower optimum soil moisture	0.4	
	SM2 = upper optimum soil moisture	1.2	
	SM3 = upper soil moisture threshold	1.6	
Temperature	DV0 = lower threshold	12	°C
	DV1 = lower optimum temperature	27	°C
	DV2 = upper optimum temperature	30	°C
	DV3 = upper threshold	34	°C
Cold stress	TTCS = cold stress temperature threshold	-18.3	°C
	THCS = temperature threshold stress accumulation rate	-0.0015	Week <sup>-1</sup>
	DTCS = degree-day cold stress threshold	–	
	DHCS = degree-day cold stress accumulation rate	–	
Heat stress	TTHS = heat stress temperature threshold	34	°C
	THHS = temperature threshold stress accumulation rate	0.055	Week <sup>-1</sup>
	DTHS = degree-day heat stress threshold	–	
	DHHS = degree-day heat stress accumulation rate	–	
Dry stress	SMDS = soil moisture dry stress threshold	0.1	
	HDS = stress accumulation rate	-0.01	Week <sup>-1</sup>
Wet stress	SMWS = soil moisture wet stress threshold	1.6	
	HWS = stress accumulation rate	0.0065	
Hot–wet stress	TTHW = temperature threshold for hot-wet stress	27	°C
	MTHW = soil moisture threshold for hot-wet stress	1.4	
	PHW = hot-wet stress accumulation rate	0.0024	Week <sup>-1</sup>
Threshold heat sum	PDD = number of degree-days above DV0 needed to complete one generation	175	°C-Days

<sup>a</sup>Values without units are dimensionless indices. The role and meaning of these parameters are described in Kriticos et al. (2015a)

*japonicus* in China, Japan and Russia (Cora et al. 2017). The CliMond global 10 min gridded climate dataset described in Kriticos et al. (2012) was used to fit parameter values. This dataset includes 30-year averages of monthly values of minimum and maximum air temperature, RH recorded at 9h00 and 15h00, and monthly rainfall total (mm). A higher resolution climate dataset (5 min gridded—HadCM3), which is available at the database of ‘CLIMEX models and projections for New Zealand’ website (<http://www.b3.net.nz/climenz/>), was used for mapping results for New Zealand.

### Growth indices

**Temperature index** Dissections conducted on parasitized *H. halys* eggs as part of studies on thermal development of *T. japonicus* (Li and Liu 2004) reported

that *T. japonicus* eggs can hatch successfully at 15 °C but cannot complete development (no adults emerge) at this constant temperature. Qiu et al. (2007) estimated that the limiting low temperature threshold for development was 12.2 °C, which was calculated using experimental data from *T. japonicus* development at temperatures ranging from 18 to 30 °C. Additionally, Li and Liu (2004) and Qiu et al. (2007) reported that *T. japonicus* developed normally at temperatures ranging from 18 to 33 °C, and optimal temperatures for development of *T. japonicus* were between 27 and 30 °C, where 100% of eggs hatched (Li and Liu 2004). Development of *T. japonicus* started to drop rapidly as temperatures rose above 33 °C, and no parasitoids were observed to have enclosed from eggs reared at 36 °C (Li and Liu 2004). Therefore, temperature index parameters were set as DV0 = 12 °C, DV1 = 27 °C, DV2 = 30 °C and DV3 = 34 °C.

**Moisture index** SM parameters are the soil moisture indices for population growth of a species. SM0 and SM3 are the limiting low and high index respectively, at below or above which no population growth takes place. SM0 was set to 0.1 to approximate permanent wilting point, which allowed population growth in the driest months (December–February) in Beijing (China). SM3 was set to 1.6 to fit the wettest locations where *T. japonicus* has been reported in southern China (e.g. wettest months in Guangzhou). SM1 and SM2 are the lower and upper optimal index, and they were set to 0.4 and 1.2 respectively.

**PDD** *Trissolcus japonicus* is expected to potentially have up to ten generations per year in Beijing, China (Qiu et al. 2007). We set the thermal accumulation parameter (PDD) to 175 degree-days to allow close to ten generations per year in Beijing, China, which is where most of *T. japonicus* current presence records have been registered (Cora et al. 2017). The base temperature was set at 12 °C (DV0).

#### Stress indices

**Cold stress** Populations of *T. japonicus* have been found to survive at colder temperatures than those reported for *H. halys* (Nystrom Santacruz et al. 2017). The cold stress threshold (TTCS) was adjusted and set to -18.3 °C taking into account the cold tolerance observed for this species, where *T. japonicus* mortality has been registered to start at temperatures ranging from -17.36 to -20.03 °C (Nystrom Santacruz et al. 2017). The accumulation rate (THCS) was iteratively adjusted to allow *T. japonicus* to barely persist in Aktach, southern Siberia, Russia (Cora et al. 2017), which is the coldest location where *T. japonicus* has been reported in Asia.

**Heat stress** The heat stress threshold (TTHS) was estimated and set to 34 °C based on the developmental studies conducted by Li and Liu (2004), and the accumulation rate (THHS) was iteratively adjusted to fit the hottest locations known to be suitable for *T. japonicus* within its humid-subtropical distribution in China and Japan.

**Dry stress** The limiting dry stress parameter (SMDS) was set to 0.1 to match the lower soil moisture threshold (SM0). Soil moisture related

stresses are likely to begin at the same soil moisture levels where plant growth stops. As plant hosts stop growing when the soil moisture drops below permanent wilting point, this is likely to impact the populations of *H. halys* and other pentatomid hosts, and hence affect *T. japonicus*.

**Wet stress** According to the subtropical known distribution of *T. japonicus* in Japan, wet stress threshold (SMWS) and its accumulation rate (HWS) were adjusted to allow persistence in all current distribution records, within Japan, presenting a humid-subtropical climate.

**Hot–wet stress** The hot–wet stress parameters (TTHD, MTHD) and the related accumulation rate (PHD) were adjusted to allow persistence of *T. japonicus* in its known range within areas with a humid-subtropical climate in Japan and China, and thus to preclude expansion into more tropical climates within south-east Asia.

#### Model validation

After fitting the parameters to known records of *T. japonicus* within China, Japan and Russia, the model was then validated by overlaying the projected CLIMEX distribution model obtained and the known occurrences in geographical areas not used for parameter fitting in its native range (i.e. South Korea, and Taiwan), and also in its most recent adventive range in the USA.

#### Potential distribution overlap of *T. japonicus* with non-target species and *H. halys* in New Zealand

The potential overlap in the distribution of *T. japonicus* with that of New Zealand's pentatomid fauna, and also with the predicted distribution of *H. halys* (Kriticos et al. 2017), was assessed by overlaying the projected CLIMEX distribution model obtained for *T. japonicus* with the current known distribution of New Zealand's non-target species, and with that of predicted by Kriticos et al. (2017) for *H. halys* respectively. Nine non-target Pentatomidae species were examined. Of these, *Cermatulus nasalis nasalis* Westwood, *C. nasalis hudsoni* Woodward, and *Oechalia schellenbergii* Guérin are predatory in the



subfamily Asopinae, and *Hypsithocus hudsonae* Bergröth, *Monteithiella humeralis* Walker, *Dictyotus caenosus* Westwood, *Glaucias amyoti* Dallas, *Cuspicona simplex* Walker, and *Nezara viridula* Linnaeus are phytophagous in the subfamily Pentatominae (Larivière 1995). Four of these species (*C. simplex*, *D. caenosus*, *M. humeralis* and *N. viridula*) are considered to have been introduced into New Zealand (Larivière 1995). The rest are considered to be either endemic (*C. nasalis hudsoni* and *H. hudsonae*) or native to New Zealand (*C. nasalis nasalis*, *G. amyoti* and *O. schellenbergii*), where native pentatomid species are also known to be present in Australia (Larivière 1995). Distribution records from all non-target pentatomid species were obtained from Larivière (1995).

## Results

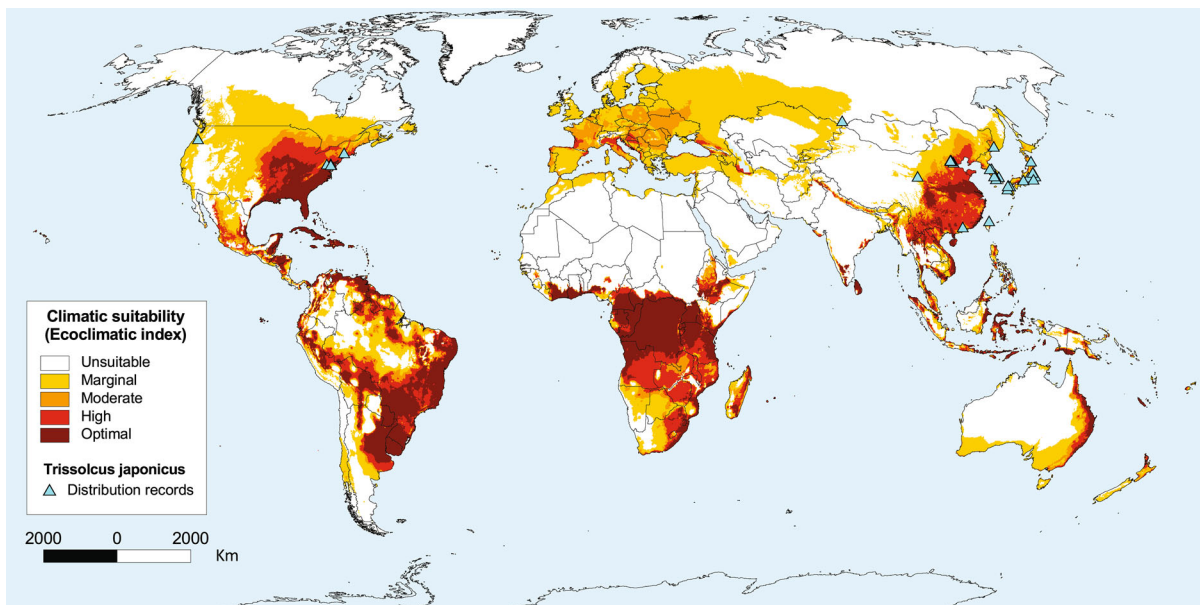
### Predicted potential distribution

The projected global potential distribution of *T. japonicus* (Fig. 1) resulting from the parameters used in our model (Table 1) shows that most of the world's Mediterranean, temperate, and subtropical climates are climatically suitable for the establishment of *T.*

*japonicus*. A few areas of semi-arid and also cool-subarctic climates are also projected to have mainly marginal suitability for the persistence of *T. japonicus* populations. The model also indicates that some tropical regions, mainly with a tropical savannah climate, may also be climatically suitable for *T. japonicus*.

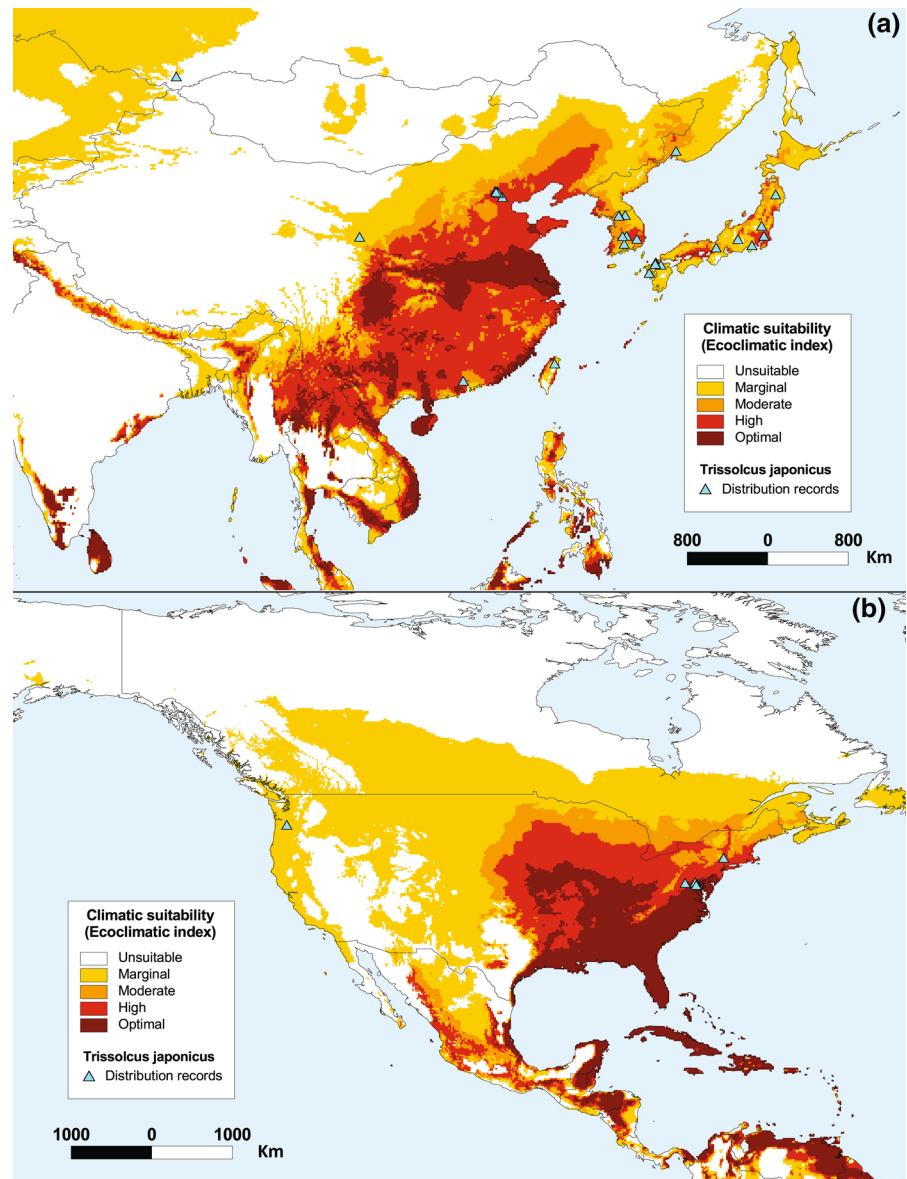
### Native range

The potential distribution of *T. japonicus* predicted by the model in its native range (Fig. 2a) is consistent with its known geographical range. The model confirmed that all areas where this species has been reported in China, Japan, Taiwan and South Korea, are climatically suitable for population persistence of *T. japonicus*. The model also projects that the parasitoid could expand its geographical range to most nearby areas with continental and subtropical climates, where most of suitable areas will range from moderate to optimal climatic suitability for the establishment of *T. japonicus* populations. The CLIMEX model also estimates that *T. japonicus* could complete close to ten generations per year in Beijing (Fig. 3). Population growth of *T. japonicus* in Beijing appears to increase from early-May until mid-August each year as a result of an increase in rainfall and rising temperatures



**Fig. 1** Modelled global climate suitability (CLIMEX Ecoclimatic Index) for *T. japonicus* to persist as a permanent population. Known current distribution is shown as point locations (triangles)

**Fig. 2** Modelled climate suitability (CLIMEX Ecoclimatic Index) for *T. japonicus* to persist as a permanent population in **a** its native range in Asia (China, Taiwan, South Korea and Japan) and adventive range in Russia, and in **b** its adventive range in the USA. Known current distribution is shown as point locations (triangles)

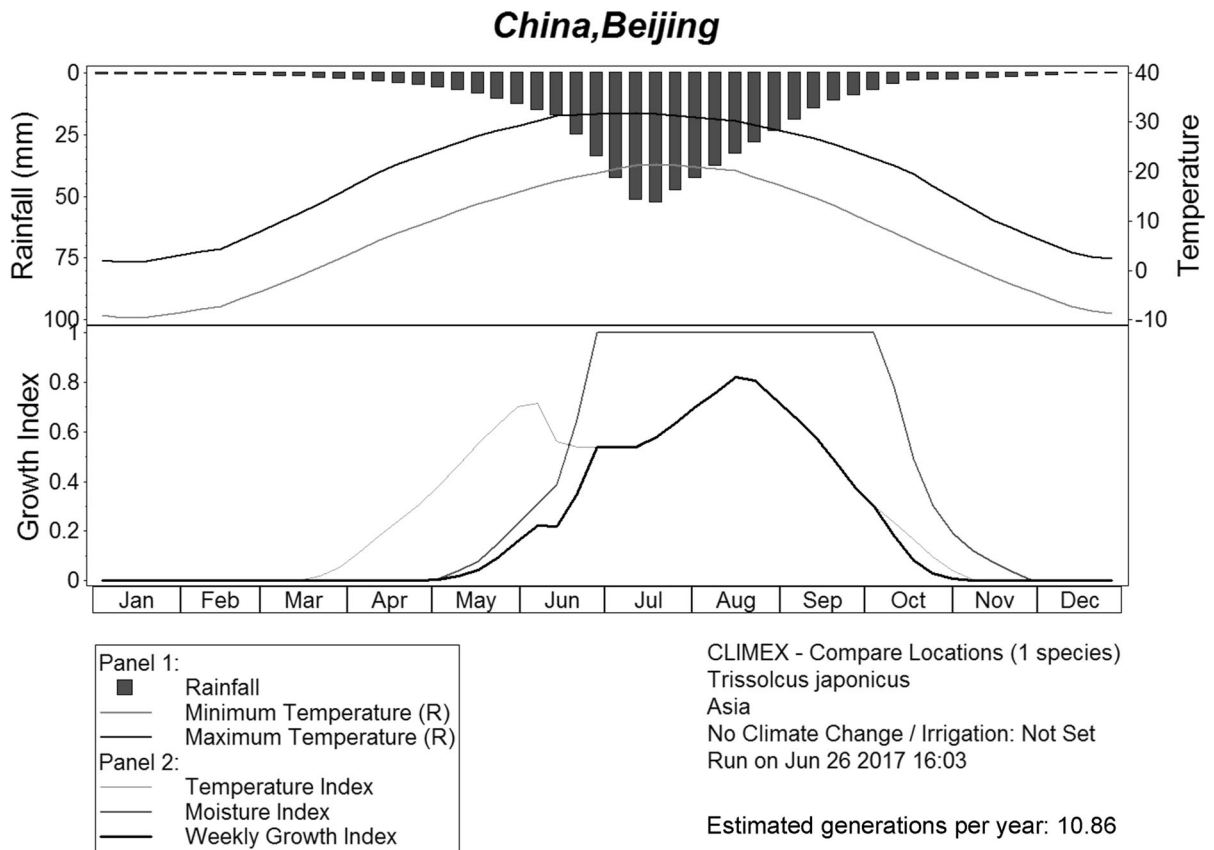


(Fig. 3). From mid-August, population growth should start dropping until late-October as a result of a sustained decrease in temperatures during these months. No population growth is expected from November to mid-March due to the dry and cold weather conditions during these months.

#### Non-native range

Validation of the CLIMEX potential distribution model fitted all observed non-native occurrences. All known presence records in the non-native range

(Russia and USA) are projected to be climatically suitable for the development of *T. japonicus*. In Russia only areas with humid-continental climates, including sites where *T. japonicus* has been recorded, are modelled as suitable for population persistence of *T. japonicus*, however these areas are only marginally suitable (Fig. 2a). All other regions in Russia are projected to be unsuitable for the establishment of *T. japonicus*, with the exception of small areas close to the border with China and North Korea, with a humid-continental climate, which are projected to have marginal or moderate climatic suitability (Fig. 2a).



**Fig. 3** CLIMEX ‘compare locations’ chart for *T. japonicus* in Beijing, China. Top panel shows weekly rainfall and maximum and minimum temperatures. Bottom panel shows CLIMEX

growth index, temperature index and moisture index. Within chart reports the estimated generations per year for *T. japonicus*

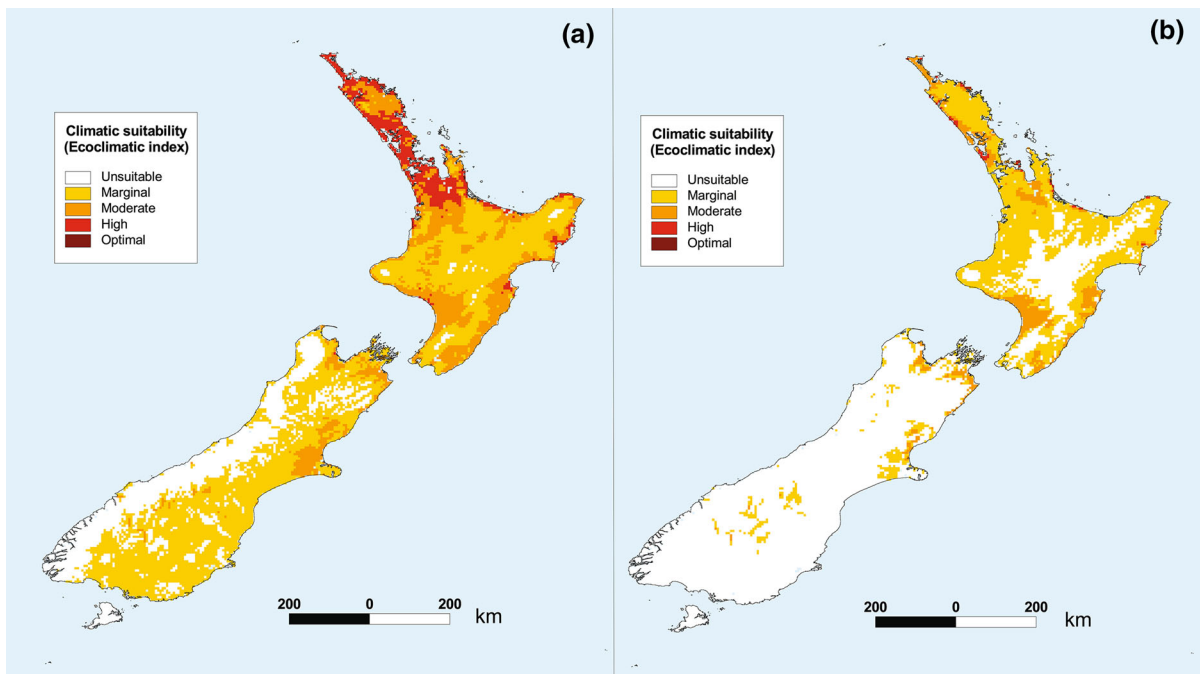
Most regions with subtropical and humid-continental climates in the eastern part of the USA are projected to be climatically suitable for *T. japonicus*, ranging mainly from high to optimal climate suitability (Fig. 2b). By contrast, most regions in the western parts of the USA with cold semi-arid, subarctic, and Mediterranean climates, are projected to be only marginally suitable (Fig. 2b).

#### New Zealand

In New Zealand, the potential distribution of *T. japonicus* covers most of the North Island and most of the northern, eastern and southern regions of the South Island (Fig. 4a), which is a much wider distribution to that of predicted by Kriticos et al. (2017) for *H. halys* (Fig. 4b). In the North Island, all northern regions (i.e. Northland, Auckland and Coromandel) are projected to range from moderate to high

climatic suitability for population persistence of *T. japonicus*, whereas most of the central and southern regions (e.g. Waikato, Taranaki, Gisborne, Hawke’s Bay) are projected to range from marginal to moderate suitability for *T. japonicus* (Fig. 4a). The CLIMEX model also estimates that *T. japonicus* could complete close to seven generations per year in Auckland compared to nearly four generations further south in Wellington (see supplementary material). *Trissolcus japonicus* population growth in Auckland is likely to start increasing steadily from early-September until mid-January each year as a result of rising temperatures. From mid-January population growth is predicted to remain constant until late-February, when it would start to drop slowly as a result of decreasing temperatures. The lowest population growth is expected in winter from mid-June to mid-August cold weather conditions during this season. In the South Island, most of the areas projected to be suitable for the





**Fig. 4** Modelled climate suitability (CLIMEX Ecoclimatic Index) for **a** *T. japonicus*, based on the parameters described in Table 1, and **b** *H. halys*, based on parameters described by Kriticos et al. (2017)

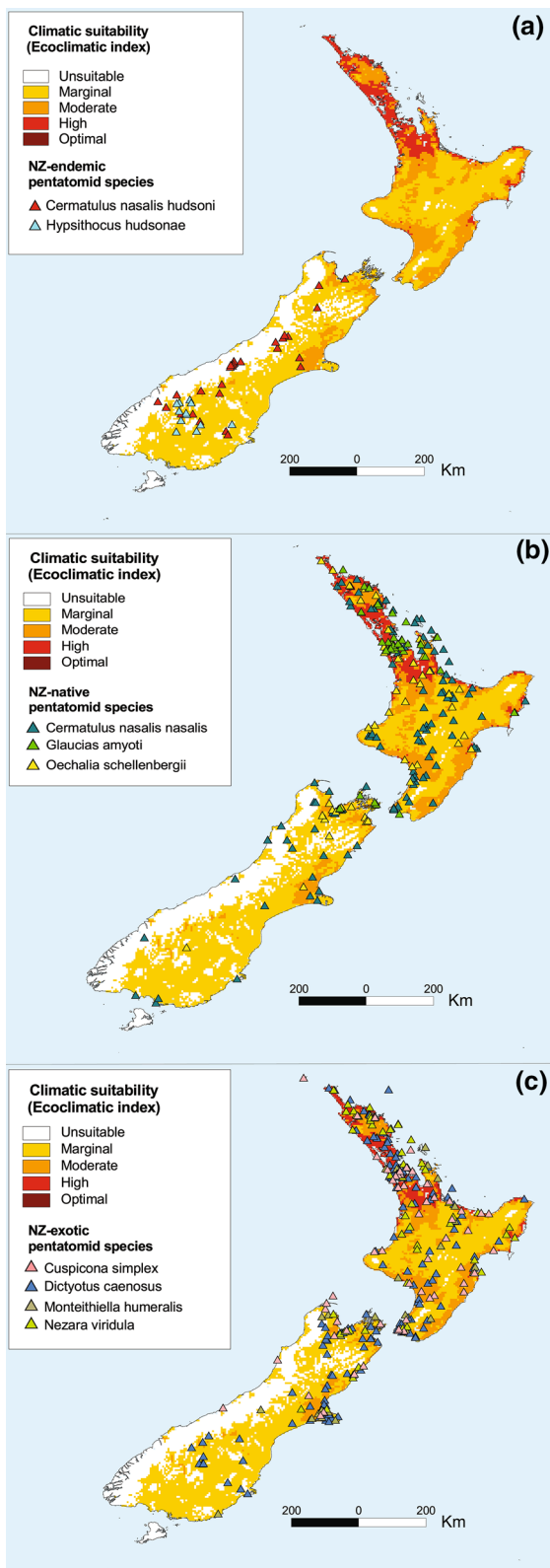
establishment of *T. japonicus* are expected to have a marginal suitability (Fig. 4a). A number of sub-alpine areas in Central Otago are estimated to be climatically unsuitable, mainly because of an inadequate annual heat sum for *T. japonicus* to complete development through one generation. Similarly, most of the West Coast region and the west side of the Southland region are projected to be unsuitable.

#### Potential distribution overlap with non-target species and *H. halys* in New Zealand

By overlaying the CLIMEX projected distribution for *T. japonicus* in New Zealand with the known distribution of New Zealand's endemic pentatomid species, *H. hudsonae* and *C. nasalis hudsoni*, an overlap can be observed in some areas of the distribution for both non-target species and that projected as suitable for *T. japonicus* (Fig. 5a). *Hypsithocus hudsonae* and *C. nasalis hudsoni* are known to occur only in sub-alpine regions in the South Island, and all areas where there is an overlap between the distribution of these two species and that of *T. japonicus* are projected to be either unsuitable or only marginally suitable for population persistence of *T. japonicus* (Fig. 5a). The

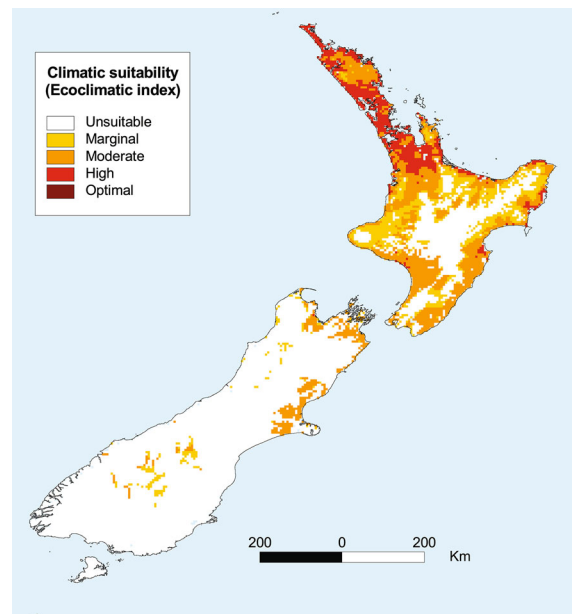
current known distribution of New Zealand's three native pentatomid species, *C. nasalis nasalis*, *G. amyoti* and *O. schellenbergii*, appears to match most of the CLIMEX projected potential distribution for *T. japonicus* in both the North and South Island. These three native pentatomids are widely distributed in the North Island, especially *C. nasalis nasalis*, and they are known to occur in a number of regions projected to have a moderate or high suitability for population persistence of *T. japonicus* (Fig. 5b). In the South Island, only *C. nasalis nasalis* is known to occur throughout the island, where it would overlap mostly with areas projected to be marginally suitable for *T. japonicus*, while *G. amyoti* and *O. schellenbergii* appear to be restricted to the northern parts of the South Island which are projected to range between marginal and moderate suitability for *T. japonicus* (Fig. 5b).

All four exotic pentatomid species are known to occur in both the North and South Island, and are expected to have a considerable overlap with the potential distribution for *T. japonicus* in New Zealand (Fig. 5c). *Dictyotus caenosus* is widespread in both the North and South Island and it is known to occur in a number of regions that are projected to range between



◀ **Fig. 5** Potential overlap between the CLIMEX projected distribution for *T. japonicus* and the known distributions of **a** endemic, **b** native, and **c** exotic Pentatomidae species in New Zealand

marginal and high suitability for *T. japonicus* (Fig. 5c). The known distribution of *C. simplex* is expected to have an overlap with most areas projected to have a moderate or high suitability for *T. japonicus* in the North Island, and mostly with areas with a moderate suitability in the South Island (Fig. 5c). Both *M. humeralis* and *N. viridula* are known to occur mostly in areas projected to be marginally or moderately suitable for *T. japonicus* in both islands (Fig. 5c). In a scenario where the establishment of permanent populations of *T. japonicus* depended on the presence of its preferred host, *H. halys*, the potential distribution of *T. japonicus* in New Zealand would be limited mostly to the North Island and a few places in the northern and eastern parts of the South Island (Fig. 6).



**Fig. 6** Modelled climate suitability (CLIMEX Ecoclimatic Index) for *T. japonicus* to persist as a permanent population in New Zealand, resulting from the intersection of Fig. 4a and 4b, based on the assumption that the parasitoid is likely to survive only in the presence of its preferred host *H. halys*

## Discussion

The CLIMEX model developed for *T. japonicus* agrees closely with the current known geographic distribution of the parasitoid in all countries within its native range (i.e. China, Japan, South Korea and Taiwan). It also suggests that *T. japonicus* is likely to not only have a broader distribution within those countries but also to have the potential to expand into other Asian countries with subtropical climates (e.g. Vietnam, Thailand, Laos, etc.) should suitable hosts be found there. However, the current distribution of *T. japonicus* in its native range may be underestimated due to lack of sampling, so new records within its native range and also from other countries where its preferred host, *H. halys*, is known to occur will be of use to further assess the model results. In terms of the global projected distribution of *T. japonicus*, the model accorded with the known adventive distribution records in Russia and the USA. In addition, the model suggested that *T. japonicus* would be able to survive in all temperate, Mediterranean and subtropical zones. Kriticos et al. (2017) used CLIMEX to estimate the potential distribution of *H. halys*, the main host of *T. japonicus*, estimating that this pest has the potential to substantially expand its current range in Europe and North America. Our CLIMEX model indicates that *T. japonicus* will also be able to thrive and expand in all places where *H. halys* is known to occur and also in most, if not all, areas where *H. halys* has been predicted to expand [see Kriticos et al. (2017) for global distribution maps of *H. halys*]. In the event that *H. halys* expands its range into novel areas, our model would provide potential biological control programmes using *T. japonicus* with valuable information to help identify climatically suitable areas for the establishment of *T. japonicus* to plan potential releases.

In New Zealand, our model indicates that suitability for population persistence of *T. japonicus* is expected to range between marginal and high in most of the North Island, and to be mostly unsuitable or marginal in the South Island. *Trissolcus japonicus* is known as a cold-tolerant species, able to survive in very low temperatures (e.g. -20.03 °C) (Nystrom Santacruz et al. 2017), suggesting that cold events will not be an impediment to its establishment in the colder regions of New Zealand (e.g. Central Otago). Compared to the potential distribution of its preferred host

*H. halys*, described in Kriticos et al. (2017), our model suggests that *T. japonicus* could have a much wider potential distribution than *H. halys* in the South Island. This is mainly because the thermal accumulation (degree-days) requirements of *T. japonicus* to complete one generation are much lower than those of *H. halys*, allowing the parasitoid to develop through many more generations than its host (Yang et al. 2009; Zhang et al. 2017).

The potential risks posed by *T. japonicus* to the non-target pentatomid species in New Zealand, based on a potential overlap between its modelled potential distribution and the known current distribution of the non-targets, varies between species. However, a number of non-climatic factors (e.g. host availability, overwintering sites, allee effects, hyperparasitoids, predators, etc.) will also affect the establishment success, survival and dispersal, and hence, the impact of *T. japonicus* on potential non-target species. For instance, most of the areas where there is an overlap between the known distributions of the endemic pentatomids *H. hudsonae* (phytophagous species) and *C. nasalis hudsoni* (predatory species) and that projected for *T. japonicus*, fall into areas projected as unsuitable or marginal for the survival of *T. japonicus*, which may initially suggest a low potential impact on these non-target species. However, the establishment of permanent populations of *T. japonicus* may also depend on the presence of its preferred host *H. halys*. In this scenario the potential distribution of *T. japonicus* in New Zealand would be limited mostly to the North Island and a few places in the South Island. Therefore, considering this potential scenario, the impact that *T. japonicus* may cause to *H. hudsonae* and *C. nasalis hudsoni* is likely to be nil.

Laboratory host specificity testing is commonly used as one of the key tools for biological control risk assessments (van Lenteren et al. 2003; Babendreier et al. 2005; Bigler et al. 2006), and it is important to mention that laboratory host specificity tests of *T. japonicus* with North American and European Pentatomidae species are currently being conducted in quarantine by USDA-ARS, CABI, and other laboratories (Zhang et al. 2017), and also with New Zealand Pentatomidae species by Plant and Food Research Ltd. Once laboratory host-testing data becomes available, the results presented in our study will provide with useful additional information of the potential risks posed by *T. japonicus* to non-target species, which will

serve as a complement to laboratory host-testing results and will help to determine more accurately the risks posed to potential non-target hosts.

CLIMEX models climate suitability only (Kriticos et al. 2015a), and it does not explicitly incorporate abiotic factors such as behaviour, habitat preference, predators, host availability and overwintering sites (Baker et al. 2000; van Driesche et al. 2008), which are also important to help predict the potential geographical distributions of species (Taylor and Kumar 2012). However, most of these factors are implicit in the distribution of the species being modelled. Inferential modelling can sometimes reveal evidence of these range-modifying factors. For example, CLIMEX modelling of the native range distribution data for *Essigella californica* revealed evidence of the existence of biotic stress factors distinguishing the aphid's fundamental and realised niches (Wharton and Kriticos 2004). Furthermore, the significant importance of irrigation as a pest risk-modifying factor has recently been revealed for weeds (Kriticos et al. 2015b), insects (Yonow et al. 2017) and plant diseases (Yonow et al. 2004). Sutherst (2003) recognises the limitations of any bioclimatic modelling exercise, and provides a template for explicit consideration of the effects of non-climatic factors on a species' ability to establish in a new area. Nevertheless, the present CLIMEX study has provided us with important information about the potential geographical distribution of *T. japonicus* in New Zealand and worldwide. This information can be used as a valuable guide for identifying areas to release *T. japonicus*, if a biological control programme should to be initiated against *H. halys*.

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