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The potential distribution of the Russian wheat aphid (*Diuraphis noxia*): an updated distribution model including irrigation improves model fit for predicting potential spread

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Abstract

Diuraphis noxia (Kurdjumov), Russian wheat aphid, is one of the world's most invasive and economically important agricultural pests of wheat and barley. In May 2016, it was found for the first time in Australia, with further sampling confirming it was widespread throughout south-eastern regions. Russian wheat aphid is not yet present in New Zealand. The impacts of this pest if it establishes in New Zealand, could result in serious control problems in wheat- and barley-growing regions. To evaluate whether *D. noxia* could establish populations in New Zealand we used the climate modelling software CLIMEX to locate where potential viable populations might occur. We re-parameterised the existing CLIMEX model by Hughes and Maywald (1990) by improving the model fit using currently known distribution records of *D. noxia*, and we also considered the role of irrigation into the potential spread of this invasive insect. The updated model now fits the current known distribution better than the previous Hughes and Maywald CLIMEX model, particularly in temperate and Mediterranean areas in Australia and Europe; and in more semi-arid areas in north-western China and Middle Eastern countries. Our model also highlights new climatically suitable areas for the establishment of *D. noxia*, not previously reported, including parts of France, the UK and New Zealand. Our results suggest that, when suitable host plants are present, Russian wheat aphid could establish in these regions. The new CLIMEX projections in the present study are useful tools to inform risk assessments and target surveillance and monitoring efforts for identifying susceptible areas to invasion by Russian wheat aphid.

Keywords: Bioclimatic model, CLIMEX, invasive species, cereals, surveillance, risk assessment

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Introduction

Diuraphis noxia (Kurdjumov) (Homoptera: Aphididae), commonly known as Russian wheat aphid, is considered one of the most damaging pests of wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*) (Hughes & Maywald, 1990; Zhang *et al.*, 2012). It is believed to be native to central-western

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Asia (Kovalev *et al.*, 1991), but now widely distributed throughout the grain-growing regions of Russia, the Middle East, Asia Minor, north-western China, Europe, Africa, the Americas (Kovalev *et al.*, 1991; Starý, 2000; Smith *et al.*, 2004; Zhang *et al.*, 2012), and most recently in Australia (Plant Health Australia, 2017; Yazdani *et al.*, 2017). In heavily infested wheat and barley crops, this aphid has been responsible for yield losses of up to 80–100% (Hughes & Maywald, 1990).

D. noxia is not known to vector viruses or pathogens but the salivary proteins *D. noxia* injects into a plant when feeding on phloem cause a severe systemic phytotoxic effect (Nicholson *et al.*, 2015), resulting in disruption of the chloroplasts and subsequent loss of chlorophyll content. Observable plant damage symptoms include longitudinal leaf rolling with white, yellow or purple streaking, trapped heads and prostrate growth (Fouché *et al.*, 1984; Burd & Burton, 1992; Mezey & Szalay-Marzsó, 2001). In parts of North America, peak abundance of *D. noxia* and associated crop damage can occur in spring and early summer, as well as late summer when the cereal crop senesces. At this time *D. noxia* shifted to non-cultivated grasses, then dispersed onto the emerging autumn-sown cereal crop (Merrill *et al.*, 2009*b*; Merrill & Peairs, 2012). In South Africa, Kriel *et al.* (1986) observed infestations occurring when adults moved from volunteer wheat or other grass hosts to an emerging wheat crop.

In some regions, *D. noxia* includes a sexual cycle in autumn where oviparous females lay overwintering eggs (holocyclic) (Zhang *et al.*, 2001, 2014). In its native range, *D. noxia* rarely reaches damaging numbers (Hopper *et al.*, 1998) which is why it is not a concern in these areas. However, *D. noxia* has caused extensive economic damage in North America and South Africa, where populations are predominantly anholocyclic (i.e. males are totally absent), overwintering as viviparous parthenogenetic females (Hewitt *et al.*, 1984; Morrison & Peairs, 1998; Merrill *et al.*, 2009*a*; Zhang *et al.*, 2014), and enabling the population to grow rapidly. Along with a high degree of phenotypic plasticity, the presence of host plants, limited diversity and abundance of natural enemies, these characteristics are likely contributing to their success to invade new habitats (Puterka *et al.*, 1993; Hopper *et al.*, 1998; Clua *et al.*, 2004; Zhang *et al.*, 2014). Estimated losses to the small grains industry in the USA were nearly one billion dollars since it was first detected in the mid-1980s (Morrison & Peairs, 1998).

D. noxia was first detected in South Australia in May 2016 (Yazdani *et al.*, 2017). It was found in cereal crops in the western half of Victoria, the Murray Region of southern New South Wales (Plant Health Australia, 2017; Yazdani *et al.*, 2017), and northern Tasmania (Plant Health Australia, 2017). It has not yet been reported in New Zealand. However, because of New Zealand's proximity to Australia and previous instances of trans-Tasman aphid dispersal from Australia to New Zealand (e.g. Close & Tomlinson, 1975), the chance of *D. noxia* arriving and establishing a population within grain-producing areas of New Zealand is a credible threat, and a major concern to producers because of expected revenue losses if it was to arrive.

Climate has long been recognised as an important environmental determinant of the geographic distribution of pest species (Kriticos *et al.*, 2012; 2013). Using meteorological data records from different locations worldwide and by weighting specific environmental factors (e.g. rainfall, minimum and maximum temperatures) (Kriticos *et al.*, 2015), climate modelling software packages are widely used to estimate the potential global distributions of pests and other species (Guisan & Thuiller, 2005; Ward, 2007; Kriticos *et al.*, 2013). Species distribution projections resulting from these climate models can be useful tools to assist with biosecurity planning and the management of pest invasions (Kriticos *et al.*, 2007). CLIMEX is well-recognised climate modelling software which has been widely used to estimate the potential distribution of insect pests (Kriticos *et al.*, 2007; Saavedra *et al.*, 2015), weeds (Kriticos *et al.*, 2003; Potter *et al.*, 2009; Watt *et al.*, 2011) and diseases (Yonow *et al.*, 2004; Watt *et al.*, 2009). 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.*, 2015).

A CLIMEX niche model by Hughes & Maywald (1990) (referred to from here on as the Hughes and Maywald model) attempted to simulate the potential distribution of *D. noxia* in Australia. However, we noticed a number of issues with their model when we compared the projected potential distribution data of *D. noxia* with its current known distribution data. The main issue was that their model did not predict a number of known locations (e.g. in Europe, the Middle East, north-western China, Australia), where *D. noxia* is present, as climatically suitable for the establishment of the aphid. Thus, the ability of Hughes and Maywald's model to inform any current decision-making on potential risk and preparedness for a potential invasion/establishment of this pest required updating.

In the present study, we used the climate modelling software CLIMEX, version 4 (Hearne Scientific Software Pty Ltd, Australia) to re-parameterise the Hughes and Maywald model and improved the fit by including presently known distribution records of *D. noxia*. We also adjusted the CLIMEX model considering the role of irrigation explicitly, thus avoiding the distortion of CLIMEX parameters (i.e. SM0: lower soil moisture threshold) that is apparent in the Hughes and Maywald model. We then examined the projected potential distribution in New Zealand from the updated CLIMEX model in relation to the ecology of *D. noxia*. Given wheat and barley are important components of primary production in New Zealand; *D. noxia* has not yet been reported in this country; and New Zealand's proximity to Australia where the aphid has recently been reported, makes New Zealand an ideal case study to assess the potential of *D. noxia* to persist as a permanent population in the country. In addition, we provide updated global predictions on the potential distribution of *D. noxia*.

Methods

The CLIMEX model

CLIMEX is a dynamic species niche model that integrates weekly responses of a population to climate and calculates a series of annual indices that allow prediction of the potential distribution of a species based on these calculations (Sutherst & Maywald, 1985; Kriticos *et al.*, 2015). CLIMEX uses an annual Growth Index (GI_A) (1) to describe the potential for population growth as a function of soil moisture and temperature during favourable conditions, and up to eight stress indices (2) and (3) to simulate the ability of the population to survive unfavourable conditions, where SI is the product of single stressors and SX is the product of combinations of stressors

(Kriticos *et al.*, 2015):

$$\mathrm{GI_A} = \frac{100}{\mathrm{S2}} \sum_{w=1}^{\mathrm{S2}} (\mathrm{TI}w \times \mathrm{MI}w) \quad (1)$$

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

$$\begin{aligned}\mathrm{SX} =&(1 - \mathrm{CDX}/100)(1 - \mathrm{CWX}/100)(1 - \mathrm{HDX}/100)\\ &(1 - \mathrm{HWS}/100)\end{aligned} \quad (3)$$

Where in (1) w is the week of the year, TIw the temperature index for week w, and MIw the moisture index for week w; (2) CS, DS, HS and WS are the annual cold, dry, heat and wet stress indices, respectively; and in (3) CDX, CWX, HDX and HWX are the annual cold–dry, cold–wet, hot–dry and hot–wet stress interaction indices.

The growth and stress indices are calculated weekly and they are combined to generate an annual index of climatic suitability called: the Ecoclimatic Index (EI) (4), which provides an overall measure of the climatic suitability of a given location to support a permanent population of the species (Kriticos *et al.*, 2015). The EI ranges from 0, for locations at which the species is not able to persist, to a theoretical maximum of 100, for locations that are climatically perfect for the species to persist (Kriticos *et al.*, 2015). However, maximum values are rare and only occur in highly stable environments, such as those found near the equator or created artificially in incubators (Sutherst & Maywald, 2005; Kriticos *et al.*, 2015). In practice, EI values greater than 20 have been demonstrated to be able to support substantial population densities (Sutherst & Maywald, 2005; Kriticos *et al.*, 2015).

$$\mathrm{EI} = \mathrm{GI_A} \times \mathrm{SI} \times \mathrm{SX} \quad (4)$$

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

The stress parameters for CLIMEX models are generally fitted to known distribution data using an iterative manual process. This involves adjusting growth and stress parameters and then comparing model results with the known distribution of the species, and including consideration of any additional information about the species being modelled, such as minimum and maximum temperatures for the development of the species (Kriticos *et al.*, 2015). In setting these parameters, consideration is also given to the biological plausibility of the selected parameters. Thus, this process allows models to be developed in accordance with the known biology of the species.

In addition, CLIMEX also includes a mechanism for defining the minimum annual developmental heat sum (degree days above the base temperature) during the growing season that is necessary for population persistence (PDD). 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 per annum needs to be completed for the species to survive in a determined location. To complete a generation, the species must reach the number of degree days set for PDD (Kriticos *et al.*, 2015).

Location records of D. noxia

Collection locations for *D. noxia* were compiled from the CABI-Invasive Species Compendium database (CABI, 2017) and from published GPS records (Puterka *et al.*, 1993; Dolatti *et al.*, 2005; Shufran *et al.*, 2007; Liu *et al.*, 2010; Ricci *et al.*, 2012; Turanli *et al.*, 2012; Zhang *et al.*, 2012; Tadele, 2015; Yazdani *et al.*, 2017). The most recent distribution records from Australia were provided by various biosecurity sources (i.e. Department of Agriculture and Fisheries Queensland; South Australian Research and Development Institute; Department of Economic Development, Jobs, Transport and Resources, Victoria; Department of Primary Industries, Parks, Water and Environment Tasmania; Department of Primary Industries and Rural Development, Western Australia).

Meteorological data

The CliMond global 10′ (spatial resolution) gridded climate dataset described in Kriticos *et al.* (2012) was used to fit parameter values under a natural rainfall scenario. This dataset includes 30-year averages of monthly values of minimum and maximum air temperature, relative humidity recorded at 09:00 and 15:00 h, and monthly rainfall total (mm). A higher resolution (5′ spatial resolution) gridded climate dataset (12ModelAvg), which is available in the database of CLIMEX models and projections on the New Zealand website (http://www.b3.net.nz/climenz/), was used for mapping results for New Zealand.

Parameters adjustment

We started with the parameter values (Table 1) published by Hughes & Maywald (1990), then using the 'Compare' module, we adjusted the parameters to fit the projected distribution of *D. noxia* to all known records in Europe, the Middle East, the USA and China under a natural rainfall scenario. Similarly to Hughes and Maywald's model, the projected potential distribution of our model could not cover a number of known location records in dry areas of north-western China. Following our initial analysis, we proposed that these dry area records might reflect populations able to persist only when irrigation is used to sustain the crop, which in turn might help to maintain a suitable microclimate in arid zones (Kriticos *et al.*, 2015).

Therefore, we decided to run the model with an irrigation scenario, so that we could assess what implications irrigation practices might have on the potential geographical distribution of *D. noxia*. We applied an irrigation scenario of 1.5 mm day^{-1} as a top-up (i.e. to increase the effective rainfall to the set amount) throughout the year, to capture the risk posed by *D. noxia* in areas where cropping could be sustained by irrigation practices (i.e. some drier regions of the world). To better define specific areas where irrigation was applied, we used an updated version of the Global Map of Irrigated Areas (GMIA) dataset (Portmann *et al.*, 2010), first produced by Siebert *et al.* (2005). This dataset allowed us to produce a composite climate suitability map, comprising of both irrigated and non-irrigated areas around the world, to show the overall projected suitability. When mapping model results, if the irrigated area was >0 for each map grid cell, then the irrigation scenario result was used. Otherwise, the natural rainfall scenario result was used.

We increased the limiting low soil moisture threshold for population growth (SM0) to just below the permanent wilting point of plants, nominally set to 0.1 (Kriticos *et al.*, 2015). The values of the lower optimum soil moisture (SM1), the upper optimum soil moisture threshold (SM2) and the limiting high soil moisture threshold (SM3) were left unchanged. The heat stress temperature threshold (TTHS) was left unchanged, but its accumulation rate (THHS) was iteratively adjusted to fit

Table 1. CLIMEX parameter values for *Diuraphis noxia*. Values for the adjusted model that differ from those of Hughes & Maywald (1990) are in bold.

Parameter	Description	Hughes & Maywald (1990) values	Adjusted values	Units[1]
Moisture	SM0 = lower soil moisture threshold	0.05	**0.09**	
	SM1 = lower optimum soil moisture	0.1	0.1	
	SM2 = upper optimum soil moisture	0.275	**0.3**	
	SM3 = upper soil moisture threshold	0.5	0.5	
Temperature	DV0 = lower threshold	3	3	°C
	DV1 = lower optimum temperature	15	15	°C
	DV2 = upper optimum temperature	25	25	°C
	DV3 = upper threshold	35	35	°C
Cold stress	TTCS = cold-stress temperature threshold			
	THCS = temperature threshold stress accumulation rate			
	DTCS = degree-day cold-stress threshold	25	25	°C-days
	DHCS = degree-day cold-stress accumulation rate	−0.00012	**−0.000105**	week^{-1}
Heat stress	TTHS = heat-stress temperature threshold	35	35	°C
	THHS = temperature threshold stress accumulation rate	0.02	**0.0015**	week^{-1}
	DTHS = degree-day heat-stress threshold			
	DHHS = degree-day heat-stress accumulation rate			
Dry stress	SMDS = soil moisture dry-stress threshold	0.05	**0.09**	
	HDS = stress accumulation rate	−0.01	−0.01	week^{-1}
Wet stress	SMWS = soil moisture wet-stress threshold	0.5	**0.6**	
	HWS = stress accumulation rate	0.035	**0.001**	week^{-1}
Hot–wet stress	TTHW = temperature threshold for hot–wet stress		**23**	
	MTHW = soil moisture threshold for hot–wet stress		**0.3**	
	PHW = hot–wet stress accumulation rate		**0.0015**	week^{-1}
Threshold heat sum	PDD = number of degree days above DV0 needed to complete one generation		**147.1**	°C-days
Irrigation scenario	1.5 mm day^{-1} as top-up throughout the year			

[1] Values without units are dimensionless indices. The role and meaning of these parameters are described in Kriticos *et al.* (2015).

the hottest locations known to be suitable for *D. noxia* within its semi-arid distribution in Iran, the hottest location where *D. noxia* was reported to be present (Dolatti *et al.*, 2005). Wet stress parameters were adjusted so as not to be limiting within the known distribution records in a number of locations in Europe (i.e. Czech Republic, Hungary and Albania) and Turkey where *D. noxia* is known to be present. Soil moisture threshold for dry stress (SMDS) was set at the same value as SM0 in our model, marginally below the permanent wilting point of plants, since the current distribution of *D. noxia* suggests that it can tolerate quite dry conditions. The cold stress degree-day accumulation rate was slightly modified from that used by Hughes & Maywald (1990) because of the inclusion of records for *D. noxia* in northern China that their model failed to predict as suitable for the aphid. The geographical range of *D. noxia* is restricted to regions of fairly moderate to low rainfall, and populations decline after heavy rainfall, suggesting that high precipitation and/or humidity may directly or indirectly reduce survival or reproduction of *D. noxia*. Therefore, hot–wet stress was used to limit *D. noxia* to its known range within Mediterranean, temperate and semi-arid climates, and to preclude the suitability of sub-tropical and tropical regions. The thermal accumulation (PDD) required for *D. noxia* to complete one generation was set to 147.1 degree days (Tazerouni *et al.*, 2013).

Model validation

Once parameters were adjusted to best fit all currently known records of *D. noxia* within Europe, the Middle East, the USA and China, the model was then validated by comparing the projected potential distribution map with the known occurrences in geographical areas that were not used for parameter fitting (e.g. Russia, Australia, central-western Asia, Africa, South America).

Results

Effect of adjusted parameters to model fit

With our adjusted model, the area climatically suitable for *D. noxia* is greater than Hughes and Maywald's model (fig. 1a, b). Differences arise from the relaxation of wet stress and the addition of hot–wet stress parameters (Table 1). The predicted climatic suitability in Europe and Australia was more restricted using the Hughes and Maywald model parameters (fig. 2a, b), mainly as a result of their modelled wet-stress accumulating rapidly at a moderate soil moisture level, well within the bounds designated as suitable for population growth. The restricted potential distributions of *D. noxia* in the Middle East and north-eastern Africa, when using Hughes and Maywald model parameters (fig. 2c), are probably due to the excessive heat-stress accumulation rate used. The adjusted heat-stress and wet-stress parameters used in our model greatly improve the overall fit of the current distribution of *D. noxia* in all the aforementioned geographic areas (fig. 2d–f). Our model also predicted that *D. noxia* could establish in south-western regions of England (fig. 2d) where wheat and barley are grown (Department for Environment Food & Rural Affairs UK, 2000). However, there are no records yet of *D. noxia* from the UK, despite its proximity to France, where established aphid populations occur.

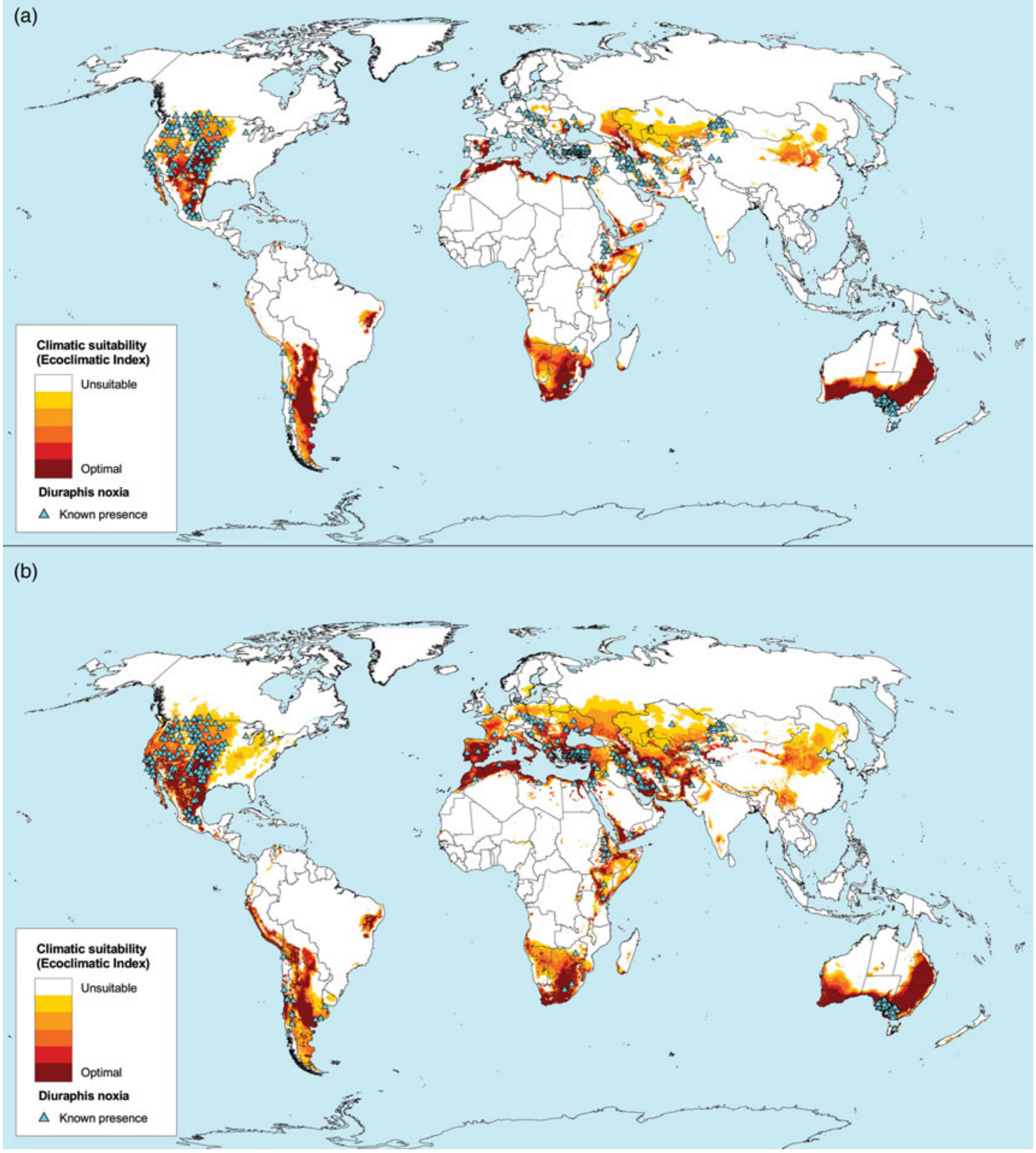

Fig. 1. Modelled global climatic suitability for *Diuraphis noxia* to persist as a permanent population as predicted by (a) Hughes & Maywald (1990) original parameters under natural rainfall, and (b) as composite of natural rainfall and irrigation based on areas identified by Siebert *et al.* (2005) using the adjusted parameters given in Table 1. Blue triangles represent current records of *D. noxia*.

Irrigation practices

Even a moderate amount of irrigation will have an effect on the potential distribution of *D. noxia*. For example, in areas where the pest is known to occur in the Middle East (e.g. Turkey and Iran; Fig. 3b), North America (e.g. the USA; Fig. 1b) and South America (e.g. Chile; Fig. 3d), dry locations modelled with a natural rainfall plus irrigation scenario increased the suitability for *D. noxia* to establish in these areas. In northern Chile and in several locations in north-western China where the aphid is known to occur, under natural rainfall conditions, the relatively dry conditions in those areas preclude the establishment and survival of *D. noxia* (fig. 3a, c). However, once irrigation is added all those locations are then projected as suitable for the establishment of *D. noxia* (fig. 3b, d).

Projection for New Zealand

In New Zealand, around 97% of wheat and 90% of barley crops are grown in the South Island where the Canterbury region grows the greatest area of wheat and barley, followed by Southland, then Otago. With our adjusted model, the area climatically suitable for *D. noxia* is greater than the one predicted

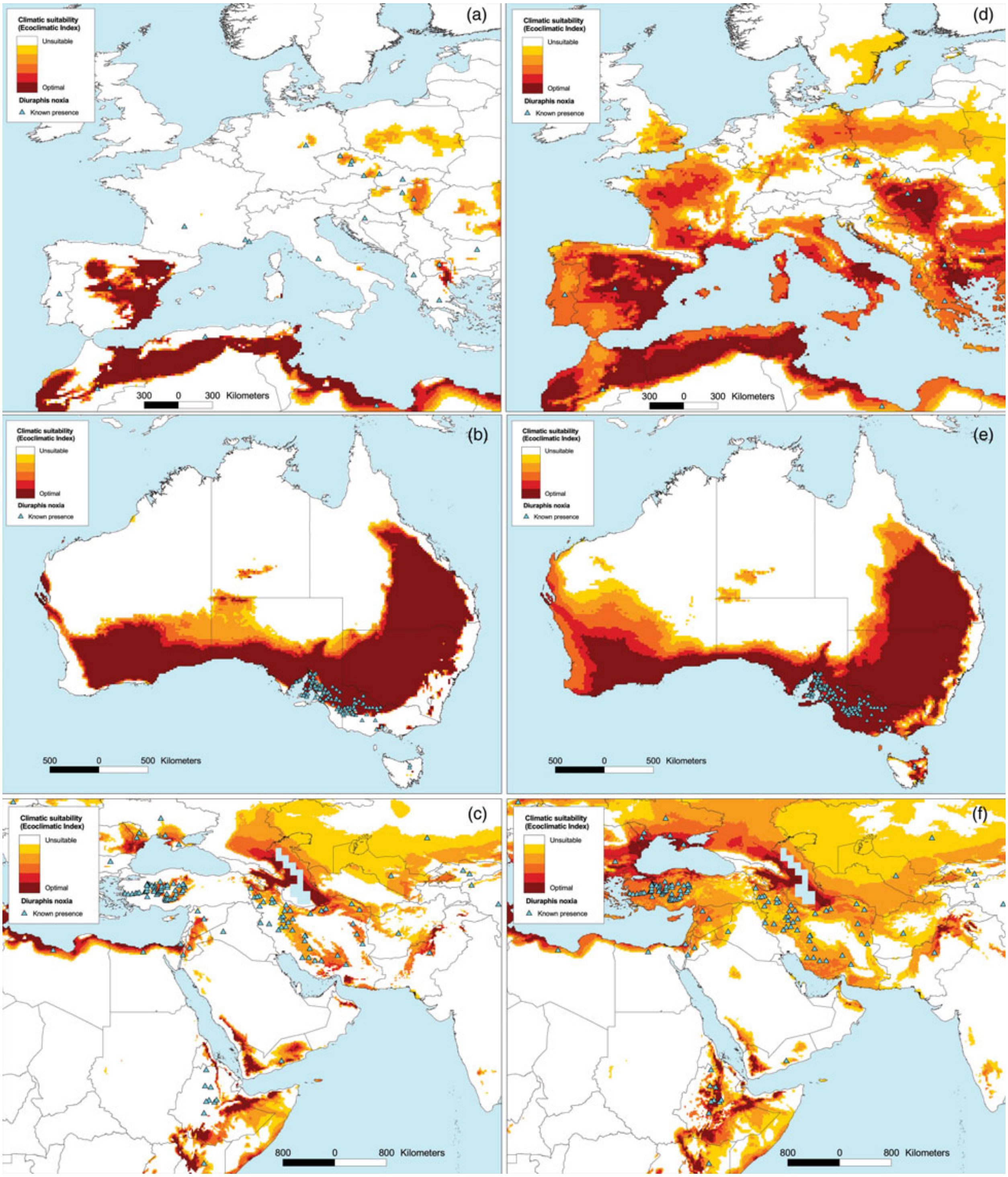

Fig. 2. Modelled climatic suitability for *Diuraphis noxia* to persist as a permanent population under natural rainfall conditions in Europe, the Middle East, North-eastern Africa and Australia as predicted by Hughes & Maywald (1990) original parameters (a–c), and as predicted by the adjusted parameters given in Table 1 (d–f). Blue triangles represent current records of *D. noxia*.

by using Hughes and Maywald's model (fig. 4a). The composite (i.e. natural rainfall plus irrigated conditions) suitability map generated with our adjusted CLIMEX model predicts the major wheat- and barley-growing region in Canterbury has a moderate to optimal climatic suitability for the establishment of *D. noxia* (fig. 4b).

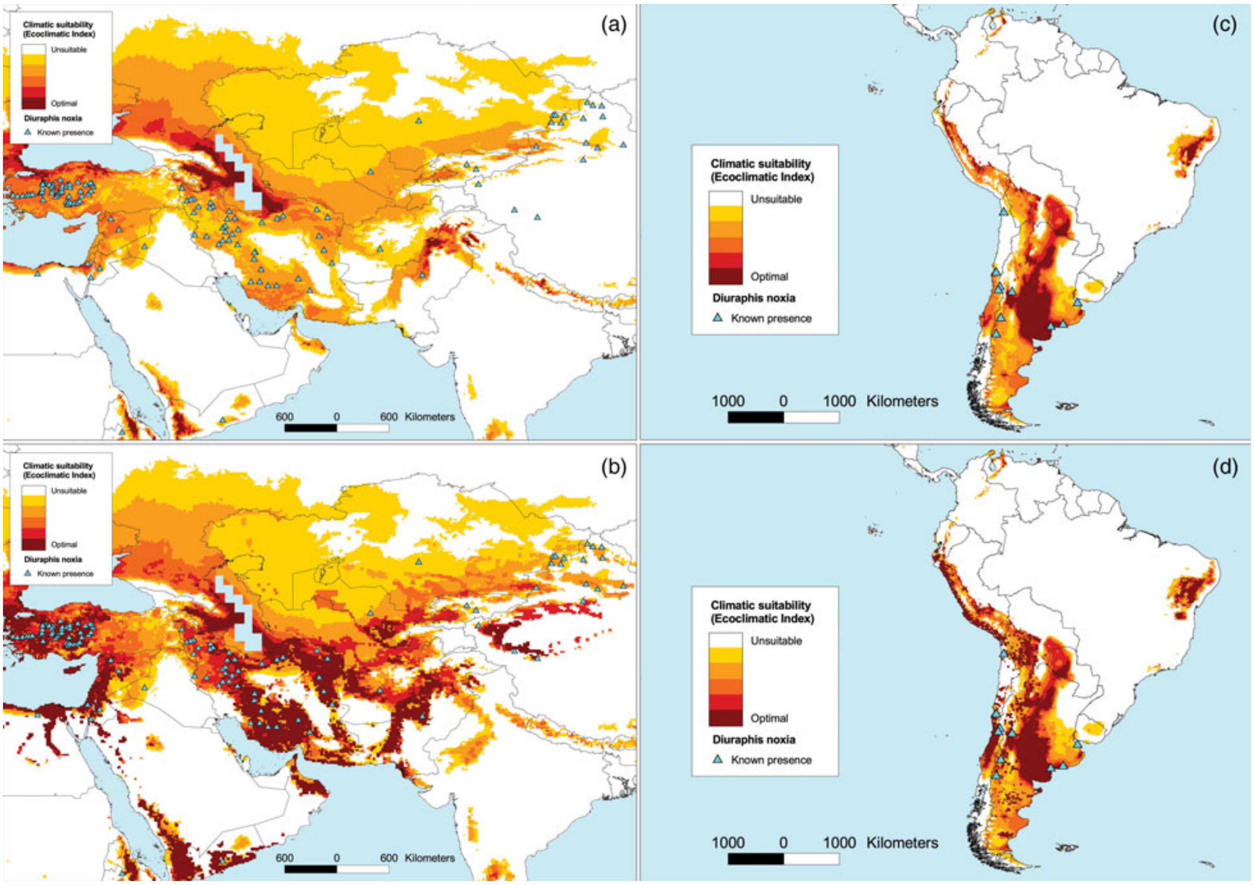

Fig. 3. Modelled climatic suitability for *Diuraphis noxia* in the Middle East, China and South America using adjusted parameters under natural rainfall conditions in (a, c), and as a composite of natural rainfall and irrigation based on the irrigation areas identified by Siebert *et al.* (2005) (b, d). Blue triangles represent current records of *D. noxia*.

Discussion

Given the current distribution of *D. noxia* globally, and based on updated parameters for the development and survival of *D. noxia* reported here, the risk of this pest potentially establishing in New Zealand as well as a number of other key cereal producing areas in Australia and worldwide is greater than predicted by the previous Hughes and Maywald's model (figs 1, 2 and 4). Although there are limitations to such climate-based models, the previous Hughes and Maywald's CLIMEX model predicted that *D. noxia* would be able to establish in Australia and this has been borne out with the recent incursion and establishment of this species in Australia (Yazdani *et al.*, 2017). The updated model reported here encompasses areas in a number of countries (e.g. Portugal, France, Italy, Albania, Greece, Turkey, Ethiopia, Australia, etc.) where *D. noxia* has been recorded outside of the original Hughes and Maywald model's boundaries, making this updated model more precise than the original model. Conversely, the updated model predicts suitable areas where *D. noxia* has not yet been reported (e.g. south-west England, Poland, parts of Australia, etc. – fig. 3b). This may due to the aphid having not yet been detected in these regions, or because it has not yet arrived, or because these areas are in fact not suitable due to variables not taken into account by the CLIMEX model. The current risk assessment of *D. noxia* in the UK has a relatively high likelihood of entry score (4 out of 5), but its risk of the establishment is considered relatively low (2 out of 5) (Anonymous, 2017). In New Zealand, the recent incursion of *D. noxia* in Australia lead to an alert being sent out to border staff by the Ministry of Primary Industries in 2016 (Anonymous, 2016), although no strategies appear to be in place to monitor risk areas that may be subject to passive wind dispersal with which the data presented here could easily assist.

A greater effort was made in Australia to assess and mitigate the risk posed by *D. noxia* (Edwards & Migui, 2005; Moir *et al.*, 2008; Plant Health Australia, 2012) and this may have been due in part to the Hughes and Maywald's model predicting its establishment in Australia. The updated model in the present study suggests the distribution of *D. noxia* could become much more widespread in Australia than previously predicted. Thus, quarantine conditions imposed on farmers and operators to prevent human-assisted movement of the pest between regions in Australia may prove ineffective where the model suggests it will be able to disperse naturally. Presently, *D. noxia* is causing the greatest damage to areas in Australia where rainfall is below 400 mm, and volunteer cereal plants such as those emerging in summer in irrigated crops seem the main summer refuge (van Helden, personal observation). The updated model provides more accurate estimates of

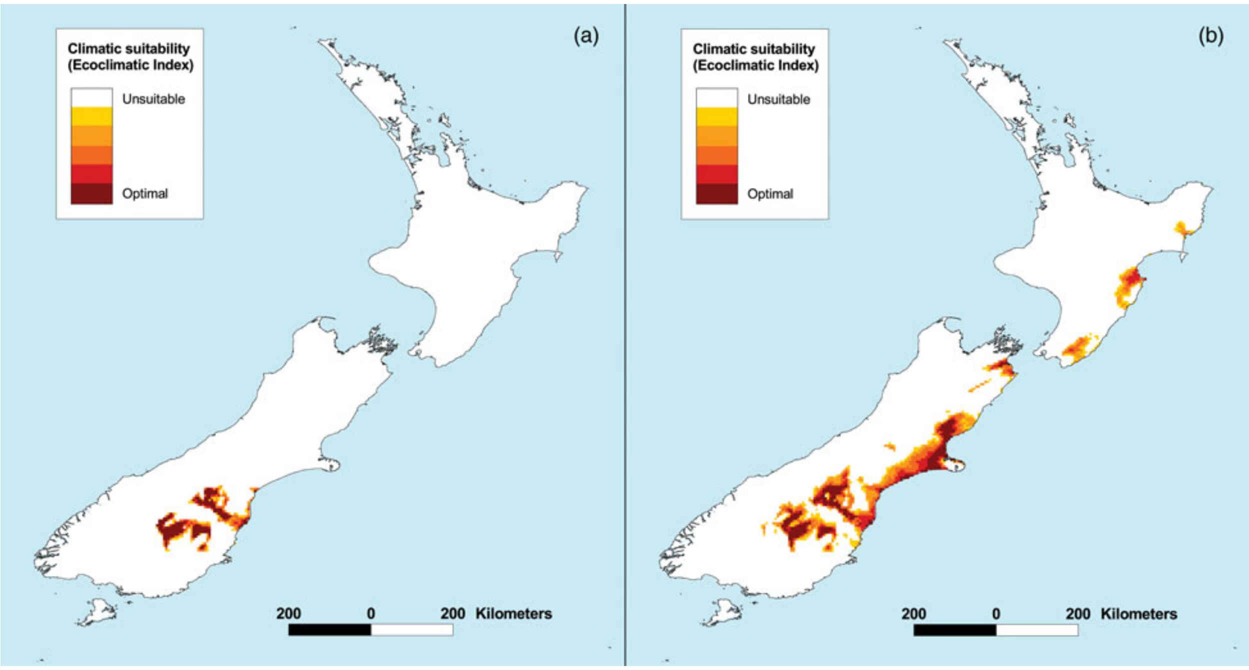

Fig. 4. Modelled climatic suitability for *Diuraphis noxia* to persist as a permanent population in New Zealand as predicted by (a) Hughes & Maywald (1990) original parameters under natural rainfall and (b) as a composite of natural rainfall and irrigation based on the irrigation areas identified by Siebert *et al.* (2005) using the adjusted parameters given in Table 1.

the risk of *D. noxia* in these drier regions of Australia. The present model could, therefore, be developed further to predict where and when populations of the pest could become economically damaging.

The information provided in the current updated model may alter the perception of the risk that *D. noxia* could establish in places such as England and New Zealand, and result in greater vigilance for this pest at the border or in areas predicted as suitable for it to establish. Whether the predicted distribution using the updated model becomes a reality for those countries and regions where *D. noxia* has not yet been reported, will require further surveillance information regarding the response of *D. noxia* to abiotic and biotic factors (e.g. overwintering temperature, rainfall, natural enemy abundance and diversity).

With regard to overwintering temperature, increased crop losses have been linked with localised populations of *D. noxia* surviving over the winter period (Merrill *et al.*, 2009*a*). Aalbersberg *et al.* (1987) observed populations of viviparous *D. noxia* increasing throughout the winter in South Africa, even with average daily temperatures of 1.5–2.8°C. Such average winter temperatures are similar or higher in many parts of Canterbury, where a large proportion of wheat and barley is grown in New Zealand, and where the updated CLIMEX model predicted the aphid could establish.

Precipitation is likely a key factor influencing *D. noxia* population growth. Models to predict *D. noxia* intensity on winter wheat crops have indicated the aphid's density is negatively related to autumn and spring precipitation, although the duration and amount of such precipitation were not elucidated (Merrill & Peairs, 2012). In a laboratory study simulating flooding events, 50% of apterous *D. noxia* survived by floating on the water surface for up to 5.5 h, while 50% of submerged aphids survived for nearly 2 h (Araya & Fereres, 1991). Evidence of the actual impact of precipitation on *D. noxia* field populations from published literature is sparse. Kriel *et al.* (1986) observed a rapid increase in *D. noxia* numbers following a sharp decline after isolated rainfall events of at least 30 mm. Field observations in South Australia reported a decline in *D. noxia* numbers after heavy rain events (duration and amount not specified) (South Australia Research & Development Institute, 2016). Hughes & Maywald (1990) reported that areas in South Africa and the USA with high rainfall (duration and amount not specified) were unfavourable for *D. noxia* infestation, and that wheat or barley growing in dry areas with 300–400 mm summer rainfall or wetter areas experiencing seasonal droughts were heavily infested by the aphid. Given the average summer rainfall in New Zealand's main wheat- and barley-growing areas is between 40 and 55 mm per month (NIWA, 2017), this is unlikely to be a limiting factor for the establishment of Russian wheat aphid in New Zealand.

The updated CLIMEX model incorporated an irrigation simulation component, a useful tool to help to refine distribution models, particularly for species where irrigation increases survival in dry areas. With regard to the impact of irrigation rates on populations of *D. noxia*, more aphids were recorded on plants maintained in a rain shelter at 15% soil water-holding capacity than on plants at 50 or 100% (Archer *et al.*, 1995). Archer and colleagues suggested *D. noxia* was much more tolerant to severe drought stress than other aphid species found on cereals (e.g. *Rhopalosiphum maidis*, *Schizaphis graminum*, *Sitobion avenae*). In our irrigation scenario in the updated model, a moderate amount of irrigation was enough to allow persistence of *D. noxia* in all dry areas located in north-western China and also in northern Chile, where the aphid is known to be present, that were previously predicted by the Hughes & Maywald (1990) model as unsuitable for the aphid's establishment.

With regard to host plants, there is no shortage of areas in New Zealand which the updated CLIMEX model has predicted as potentially suitable for *D. noxia* establishment. In addition to barley and wheat, other cultivated cereals considered primary host plants of *D. noxia* include rye (*Secale cereale*), oats (*Avena sativa*) and triticale (*Triticosecale* spp.). Volunteer plants of cereals, such as wheat and barley, are considered important hosts for *D. noxia* especially when cereal crops are senescing (Hewitt *et al.*, 1984; Armstrong *et al.*, 1991; Brewer *et al.*, 2000). Other host plant species found throughout the cereal-growing regions in New Zealand that have been shown to maintain reproducing females or were found with *D. noxia* on them include: *Bromus willdenowii*, *Cynondon dactylon*, *Dactylus glomerata*, *Echinochloa cruss-galli*, *Festuca rubra*, *Lolium multiflorum*, *L. perenne*, *Panicum capillare*, *Poa pratensis*, *Vulpia myuros* (Kindler & Springer, 1989; Armstrong *et al.*, 1991; Edgar & Connor, 2000; Champion, 2012). Thus, availability of host plants is unlikely to be a limiting factor for the establishment of *D. noxia* in New Zealand.

Natural enemies may also play an important role in the success of an insect species establishing populations in a new region (Hopper *et al.*, 1998). The natural enemies associated with *D. noxia* (Halbert & Stoetzel, 1998) which are already present in New Zealand include the hymenopteran parasitoids: *Diaeretiella rapae*, *Aphelinus asychis*, *Aphidius colemani*, *A. rhopalosiphi* and *Ephedrus plagiator*. Of the natural enemies known to be associated with *D. noxia*, *D. rapae* was the most commonly found parasitoid attacking Russian wheat aphid in the USA (Pike *et al.*, 1997; Bosque-Pérez *et al.*, 2002) and Australia (Heddle & van Helden, 2016). Amongst the coccinellids associated with *D. noxia*, *Adalia bipunctata* and *Coccinella undecimpunctata* are extant in New Zealand. In addition, native insect predators present in New Zealand may adapt to predating on *D. noxia*. These include the brown lacewing (*Micromus tasmaniae*), syrphids (*Melangyna novaezelandiae* and *Melanostoma fasciatum*) and nabids (*Nabis capsiformis*, *N. kingbergi* and *N. maoricus*) (Stufkens & Farrell, 1989; Thomas, 1989; Fagan *et al.*, 2010).

A good understanding of the variables that define the geographical distributions of invasive species is essential for accurately predicting their future dispersal, establishment and range (Taylor & Kumar, 2012). Furthermore, abiotic factors and dispersal mechanisms play an important role in predicting the rate of colonisation of invasive alien species into new areas (Taylor & Kumar, 2012). In these respects, CLIMEX may have some restrictions because it uses only climate-related features and meteorological data (Kriticos *et al.*, 2015) and it does not incorporate non-climatic factors (Baker *et al.*, 2000). 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* conducted by Wharton & Kriticos (2004) revealed evidence of the existence of biotic stress factors distinguishing the aphid's fundamental and realised niches. Furthermore, the significant importance of irrigation as a pest risk-modifying factor has recently been revealed for weeds (Kriticos *et al.*, 2015), insects (Yonow *et al.*, 2017) and plant diseases (Pardey *et al.*, 2013). Nevertheless, the present CLIMEX study has provided us with important updated information about the potential geographical distribution of *D. noxia* worldwide and in New Zealand.

The new potential geographic distribution model for *D. noxia* using our updated CLIMEX parameters can be used to identify areas susceptible to invasion by *D. noxia*, to assist with biosecurity planning (e.g. focusing surveillance effort, identifying potential pathways and undertaking industry risk assessment). Despite the foreknowledge provided by a model predicting its establishment in Australia, *D. noxia* was not detected in time to eradicate (Yazdani *et al.*, 2017). Thus, detection technology and strategies for species such as *D. noxia* will need to improve to increase the chances of preventing establishment in new regions. Should *D. noxia* become established, the updated CLIMEX model could also aid in its management by providing knowledge of where the aphid could have the greatest economic impact. The updated CLIMEX model suggests *D. noxia* would be able to establish in all major wheat- and barley-growing regions in New Zealand. However, local abiotic and biotic factors such as high precipitation and natural enemies could limit the ability of *D. noxia* to establish permanent populations in some areas of New Zealand; further study is warranted to elucidate their impacts. Likewise, further examination of these factors could help to determine whether *D. noxia* may establish in the other regions predicted by the updated model where this species has not yet been found allowing producers, industry and governments time to take preventative actions.

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