Prediction of the Potential Geographic Distributions and Risk Assessment of Four Trade Impacting Invasive Insect Pests in Australia and China

by

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Thesis Declaration

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Abstract

This thesis explores biological invasion through the potential pest distribution and risk analysis of tomato potato psyllid (TPP), *Bactericera cockerelli*; fall armyworm (FAW), *Spodoptera frugiperda*; *Bactrocera bryoniae;* and *Bactrocera neohumeralis*. Through better understanding of the pest distribution and risk analysis agricultural management policies can be implemented, and containment and eradication actions taken.

The TPP is a psyllid native to North America that has recently invaded Australia. The potential for economic losses accompanying invasions of TPP and its associated bacterial plant pathogen *Candidatus* Liberibacter solanacearum (CLso), has caused much concern. Here, we employed ecological niche models to predict environments suitable for TPP/CLso on a global scale and then evaluated the extent to which global potato cultivation is at risk. A total of 86 MaxEnt models were built using various combinations of settings and climatic predictors, and the best model based on model evaluation metrics was selected. Climatically suitable habitats were identified in Eurasia, Africa, South America, and Australasia. Intersecting the predicted suitability map with land use data showed that 79.06% of the global potato production, 96.14% of the potato production acreage in South America and Eurasia, and all the Australian potato production are at risk. The information generated in this study increases knowledge of the ecology of TPP/CLso and can be used by government agencies to make decisions about preventing the spread of TPP and CLso across the globe.

Fall armyworm (FAW), *S. frugiperda* is native to the Americas and it has rapidly invaded 47 African countries and 18 Asian countries since the first detection of invasion into Nigeria and Ghana in 2016. It is regarded as a 'super pest' based on its host range (at least 353 host plants), its inherent ability to survive in a wide range of habitats, its strong migration ability, high fecundity, rapid development of resistance to insecticides/viruses and its gluttonous characteristics. In order to better understand the seasonal geographic distributions of *S. frugiperda*, we employed ecological niche models of MaxEnt to predict potential year-round breeding and seasonal distribution for *S. frugiperda* on a global scale and in Australia. A total of 74 MaxEnt models were built using various combinations of regularization multiplier, feature class and climatic variables, and the best model based on model evaluation metrics was selected, with an evaluation of dominant climatic factors that control its distribution. The

results suggest that the temperature factor was the most important variable affecting the seasonal distribution of *S. frugiperda*. No matter where in the world, the year-round breeding distribution model predicted smaller portions of fall armyworm's ranges than the seasonal model. *S. frugiperda* had a high remaining invasion potential in Australia, posing a significant threat to its biosecurity, food security and agricultural productivity.

Bactrocera bryoniae and *Bactrocera neohumeralis* are highly destructive fruit flies and considered major biosecurity/quarantine pests of fruit and vegetable in the tropical and subtropical regions in the South Pacific. Ecological niche modelling MaxEnt was employed to predict the potential geographic distribution of *B. bryoniae* and *B. neohumeralis* across the world and particularly in China with the occurrence data of these two species. *B. bryoniae* and *B. neohumeralis* exhibit similar potential geographic distribution ranges across the world and in China, and included southern Asia, the central and the southeast coast of Africa, southern North America, northern and central South America, and Australia. While within China, most of the southern Yangtze River area was found suitable for these two species. Notably, southern China was considered to have the highest risk of *B. bryoniae* and *B. neohumeralis* invasions. Our study identifies the regions at high risk for potential establishment of *B. bryoniae* and *B. neohumeralis* in the world and particularly in China and informs government officials to develop policies for inspection and biosecurity/quarantine measures to prevent and control their invasion.

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Abbreviations

ABER	Agricultural Block Exemption Regulation
ARM	Agricultural Risk Management
AUC	under the curve
BIC	Bayesian Information Criterion
BIOCLIM	Bioclimatic Prediction System
Bt	Bacillus thuringiensis
B3	Better Border Biosecurity
CABI	Centre for Agriculture and Biosciences International
CCC	Commodity Credit Corporation
CGE	Computable General Equilibrium Modelling
CIE	Centre for International Economics
CLIMEX	Climate Change Experiment
CLso	*Candidatus* Liberibacter Solanacearum
COI	cytochrome oxidase subunit I
C-strain	corn strain
DPIRD	Department of Primary Industries and Regional Development
ELAP	Emergency Assistance for Livestock, Honeybees, and Farm-Raised Fish Program
ENMs	ecological niche models
EPPO	European and Mediterranean Plant Protection Organization
EPPRD	Emergency Plant Pest Response Deed
EPPs	Emergency Plant Pests
FAO	Food and Agriculture Organization
FAW	Fall armyworm
GAM	Generalized Additive Model
GARP	Genetic Algorithm for Rule-Set Production
GDP	Gross domestic product
GHS	Globally Harmonized System
GLM	Generalized Linear Model

HHPs	highly hazardous pesticides
IAS	Invasive alien species
IBPs	Industry Biosecurity Plans
I-O	Input - Output Analysis
IPPC	International Plant Protection Convention
ISPM	International Standard for Phytosanitary Measures
LFP	Livestock Forage Program
LIP	Livestock Indemnity Program
MaxEnt	Maximum Entropy
MESS	multivariate environmental similarity surface
MTP	minimum training presence threshold
NAP	Noninsured Crop Disaster Assistance Program
ORC	Owner Reimbursement Costs
PB	Partial Budgeting
PCA	principal component analysis
PE	Partial Equilibrium Modelling
PHA	Plant Health Australia
PRA	Pest Risk Analysis
PY	Psyllid Yellows
RA	Risk Assessment
RADAR	Rapid Agricultural Disaster Assessment Routine
ROC	receiver operating characteristic curve
RR	resistance ratios
R-strain	rice strain
Tpi	triose-phosphate isomerase
TPP	Tomato Potato Psyllid
USDA	U.S. Department of Agriculture
VE	vegetative emergence
WHO	World Health Organization
ZC	Zebra chip

Chapter One

Status and perspective of global biological invasions and plant biosecurity

1.1 Status and perspective of global biological invasion

1.1.1 Status of global biological invasions

Economic globalization and human activities have extensively increased the spread of species from one place to another in the past century. More frequent interactions between people and countries, together with more complex transportation facilities have promoted the rapid spread of species, that in turn have colonized new regions and environments, via international trade, tourism and transportation (Wan *et al.* 2008, Horvitz *et al.* 2017). The exchange and migration of species (referred to as invasive alien species (IAS)) between continents has been accelerating with increasing risk of biological invasions (Seebens *et al.* 2017).

Invasive alien species have presented large threats to economies, environments, and human-being welfare. At the same time, modern agricultural production (including agriculture, forestry, animal husbandry and aquaculture etc) have relied partly on introduction and exchange of alien species (Cook *et al.* 2011). The deliberate sharing of biological diversity brings enormous economic benefit as well as concomitant hazards of IAS. IAS are a major cause of crop loss and do adversely affect food security (Cook *et al.* 2011). Biological invasion is a significant concern for governments, due to the potential economic damage it causes (Lodge *et al.* 2000). Economic costs of IAS have been estimated to be almost 5% of global GDP (2016) (IUCN, 2016), with IAS alone estimated to cost the global economy more than US$ 70 billion per year (IUCN, 2017). In the United States alone, crop and forest production losses from invasive insects and pathogens have been estimated at US$40 billion per year (Pimentel *et al.* 2005). In Australia, IAS have been identified as a significant economic burden with a combined estimated cost (economic losses and control) of $9.8 billion (2001–2002, Australian Bureau of Statistics, 2002), rising to $13.6 billion in the year 2011–2012 (Australian Bureau of Statistics, 2012).

The global impacts of IAS are substantial and costly following invasions in agriculture and the environment (Pimentel *et al.* 2005; Stohlgren and Schnase 2006; Kettunen *et al.* 2008; Ricciardi *et al.* 2011 Wan *et al.* 2008; Wan *et al.* 2017).

Research plays a critical role in the management of IAS as it is the solution in which new information is obtained and communicated. Compliance with strategy frameworks for research capacity building has led to a series of research programs being launched by different ministries in different countries. Generally, these programs can be classified into two types; fundamental research and applied research. During the past 20 years, the number of publications in the field of biological invasions (study of IAS) increased rapidly in many countries. In total, 57,268 articles on biological invasion were published based on literature indexed by the Web of Science during 1998-2017 (Figure 1-1). The number of published papers show a steady upward trend from 2002 to 2017, gradually increasing from 1131 to 5720 (Figure 1-1). In each country, the numbers of published papers in biological invasions have gradually increased from 2002 to 2017 (Figure 1-2). In total, the largest number of papers published come from the United States with a total of 20749 in the past two decades, followed by Australia with a total of 5110, and then Canada and England, with a total of 3523 and 3325, respectively (Figure 1-2).
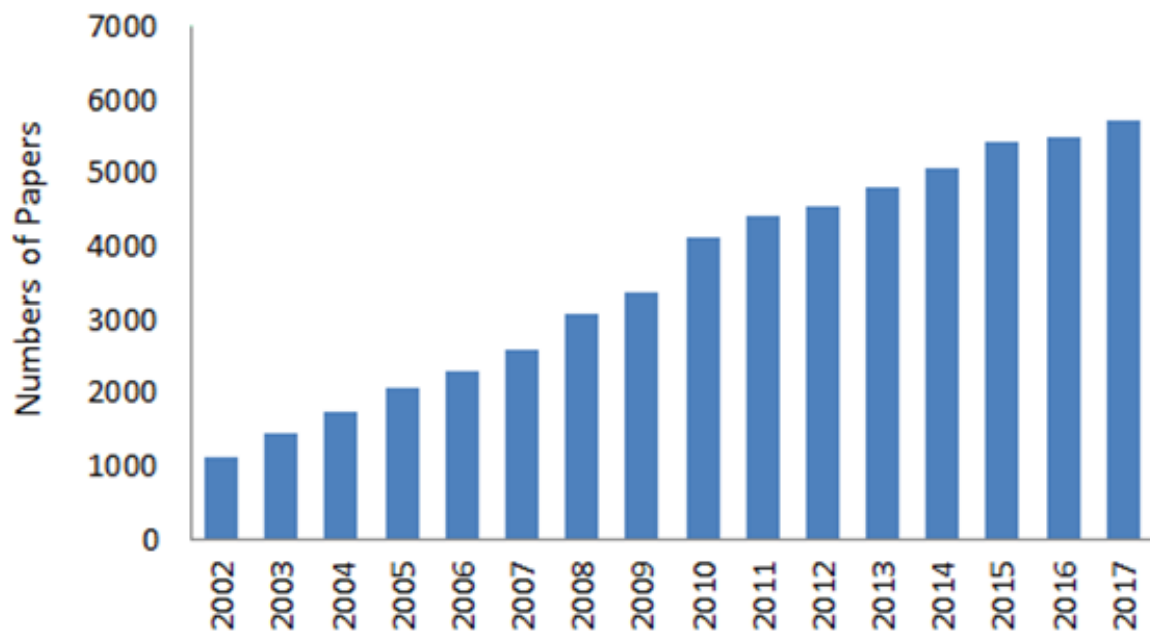
Figure 1-1. The number of papers on biological invasions around the world during 2002-2017.
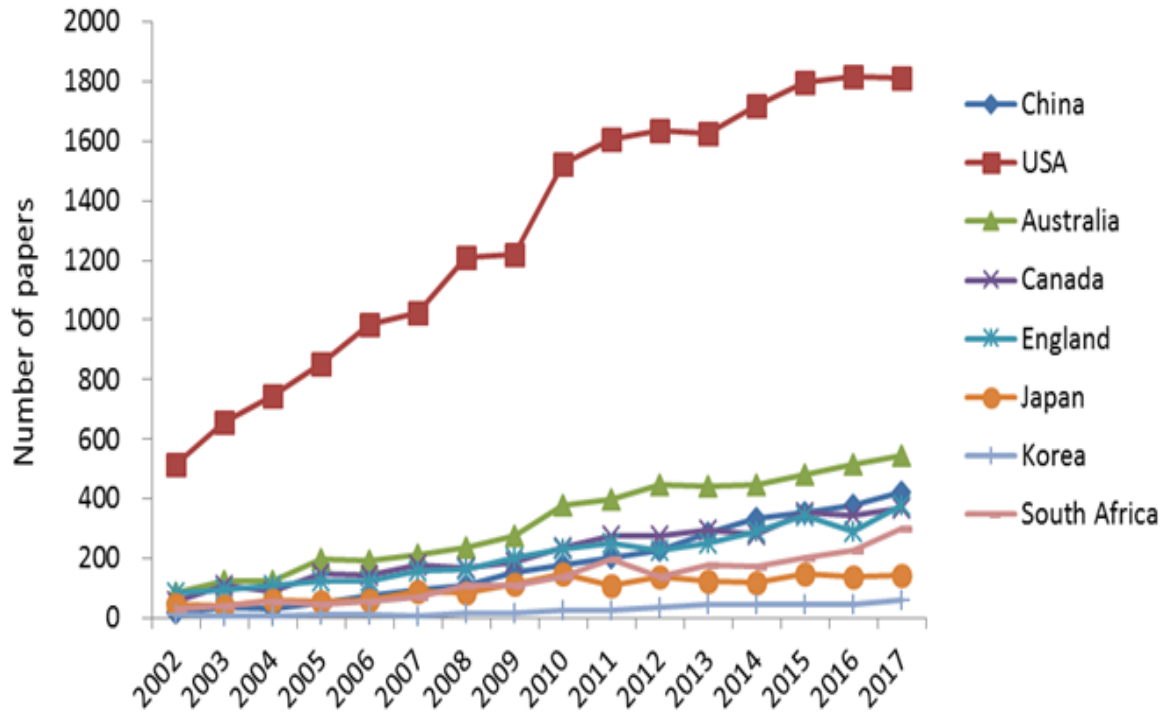
Figure 1-2. The number of papers on biological invasions published by different countries during 2002-2017.

1.1.2 Prevention and control system in global biological invasions – country perspectives

1.1.2.1 New Zealand

New Zealand is a geographically isolated archipelago and this is the reason the country is free from many pests and diseases that damage production and natural ecosystems or endanger human and animal health. However, in order to maintain this geographical location advantage research has been activated to strengthen international trade from New Zealand (Munyaneza 2010). The Better Border Biosecurity (B3) project was initiated, which is a multi-partner, cooperative science collaboration that aims to develop approaches and tools to ensure harmful organisms are kept out of New Zealand, or, if they do manage to enter, are eradicated before establishing permanent populations (Teulon *et al*. 2009).

1.1.2.2 Australia

The Department of Agriculture, Water and Environment administers the Biosecurity Act 2015, Export Control Act 1982, Imported Food Control Act 1992 and various other Acts in order to protect Australia's animal, plant and human health status and to maintain market access for

Australian food and other agricultural exports. The Biosecurity Act 2015 focuses on how to manage biosecurity threats to crops, animal and human heath in Australia and its external territories. Its emphasis is on a balance between protecting Australia from pests and diseases (including biological invasions), and maintaining our ability to trade internationally, and the shared responsibility of all citizens. Most biosecurity management functions are governed and administered by the Australia Government, State and Territory governments, while the agricultural industry and communities also plays an important role (MacLeod 2015).

1.1.2.3 China

China has been one of the countries severely damaged by IAS, which occur in almost all ecosystems. Since the beginning of the twenty-first century, China has invested considerable resources in basic and applied IAS research to meet the urgent needs in terms of prevention and management. This research has led to a series of policies, measures and action plans that have been formulated to prevent and control IAS (Wan *et al*. 2017). For example, Law of People's Republic of China on the Entry and Exit Animal and Plant Quarantine (1991), Frontier Health and Quarantine Law of the People's Republic of China (1986, 1992), and Import and Export Animal and Plant Quarantine Regulations of the People's Republic of China (1982) (Wan *et al*. 2008). Recently, Chinese scientists have come up with the 4E actions on biological invasions in China that aims to provide effective tactics and action for IAS management based on the Comprehensive consideration of invasive time and cost, as well as population size and damages (Wan *et al.*2016a, Wan *et al*. 2016b). 4E actions include four steps, such as Early Warning & Prevention (E1), Early Monitoring & Rapid Detection (E2), Early Eradication & Blocking (E3), and Entire Mitigation (E4) (Figure 1-3) (Wan *et al*. 2008).

Figure1-3. Early Warning & Prevention (E1), Early Monitoring & Rapid Detection (E2), Early Eradication & Blocking (E3), and Entire Mitigation (E4). 4E actions on biological invasions in China (Wan *et al.* 2008).

1.1.2.4 Similar IAS risks that both Australia and China face

China's agriculture structures are obviously complementary to Australia's and this has led to the establishment of close international trade relations (Wan *et al.* 2008). Since 2011, China has become the largest targeted market for Australia's agricultural exports, fishery and forestry products as well as wheat, barley, oats, wool, cotton, rapeseed oil, timber and other agricultural and forestry products (Zhou 2014). To ensure the bio-ecological security of the two countries, establish stable trade relations, and improve the social and economic development level of the two countries it is important to understand the research status and focus point similarities for biological invasion between China and Australia (Black and Bartlett 2020).

Bactrocera bryoniae and *Bactrocera neohumeralis* (Diptera: Tephritidae) are highly destructive and major biosecurity risk pests of fruit and vegetable in the tropical and subtropical regions in the South Pacific, China and Australia (Wan *et al.* 2020). It's noteworthy that Australia and China list similar IAS threats such as *Bactrocera albistrigata*, *Bactrocera carambolae*, *Bactrocera umbrosa*, *Bactrocera zonata*, and *Bactrocera papaya*. *Bactrocera* spp.

are native to tropical Asia, Australia and the South Pacific regions (White and Elson-Harris 1992), and now dominate the top of the invasive lists for Australia and China.

1.1.3 Status and perspective of biological invasions in Australia

1.1.3.1 Ecosystem in Australia

Australia is a sovereign country comprising the mainland of the Australian continent, the island of Tasmania and numerous smaller islands. It is the largest country in Oceania and the world's sixth-largest country by total acreage. The climate of Australia is significantly influenced by ocean currents, including the Indian Ocean Dipole and the El Niño–Southern Oscillation, which is correlated with periodic drought (Rachel 2007; Kathy 2007) (Figure 1-4). While most of Australia is semi-arid or desert, it also includes a diverse range of habitats from alpine heaths to tropical rain forests. Driven by the continent's age, extremely variable weather patterns, and long-term geographic isolation, Australia has a broad range of biodiversity including many native plants and animals that live nowhere else on Earth (Plant Health Australia, 2013). For example, fungi typify diversity with an estimated 250,000 species present in Australia but — of which only 5% have been described—occur (Pascoe 1991). About 85% of flowering plants, 84% of mammals, more than 45% of birds, 89% of in-shore and temperate zone fish are unique only to Australia (National Plant Biosecurity Status Report, 2017). Therefore, biological invasion is considered one of the greatest threats to biosecurity and eco-security of Australia.
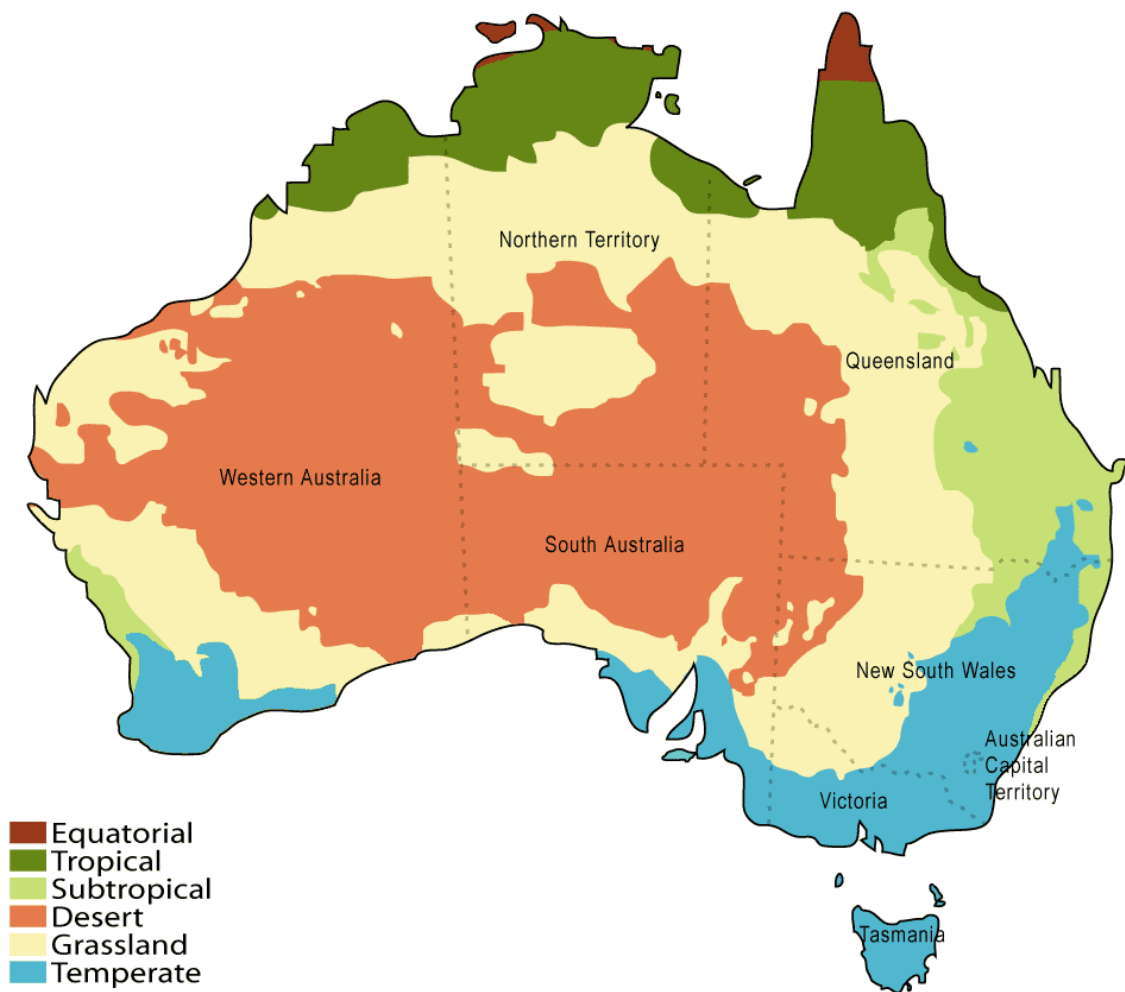
Figure 1-4. Climate map of Australia, based on Köppen classification (from National Plant Biosecurity Status Report, 2017).

1.1.3.2 Agriculture in Australia

According to the Australian Bureau of Statistics 2017, Australia's major agricultural trade partners are with China, Japan and the United States. More than 325,300 people are employed in Agriculture, forestry and fishing (Australian Bureau of Statistics, 2017). The gross profit from agriculture and its related sectors is ~$155 billion Australian dollars per year which accounts for approximately 12% of national GDP. Almost half of Australia's total land area is used for agriculture. In 2015–16, around 371 million hectares was farmed by 85,681 crop and livestock businesses, all of whom depend on plant production to some extent (Australian Bureau of Statistics, 2017). Furthermore, due to wide climate variability across Australia, producers grow a variety of crop species, each of which has a unique set of pests that pose a threat to production. For example, bananas, sugarcane, pineapples, mangoes and ginger are

grown in the tropical and sub-tropical north, while stone fruits, grapes, nuts, onions and potatoes can be cultivated in more southern temperate zones. Vast areas are suited to broad acre production of grains, pulses, cotton, forestry, and pasture for livestock production, and vegetables are grown in many areas (National Plant Biosecurity Status Report, 2017).
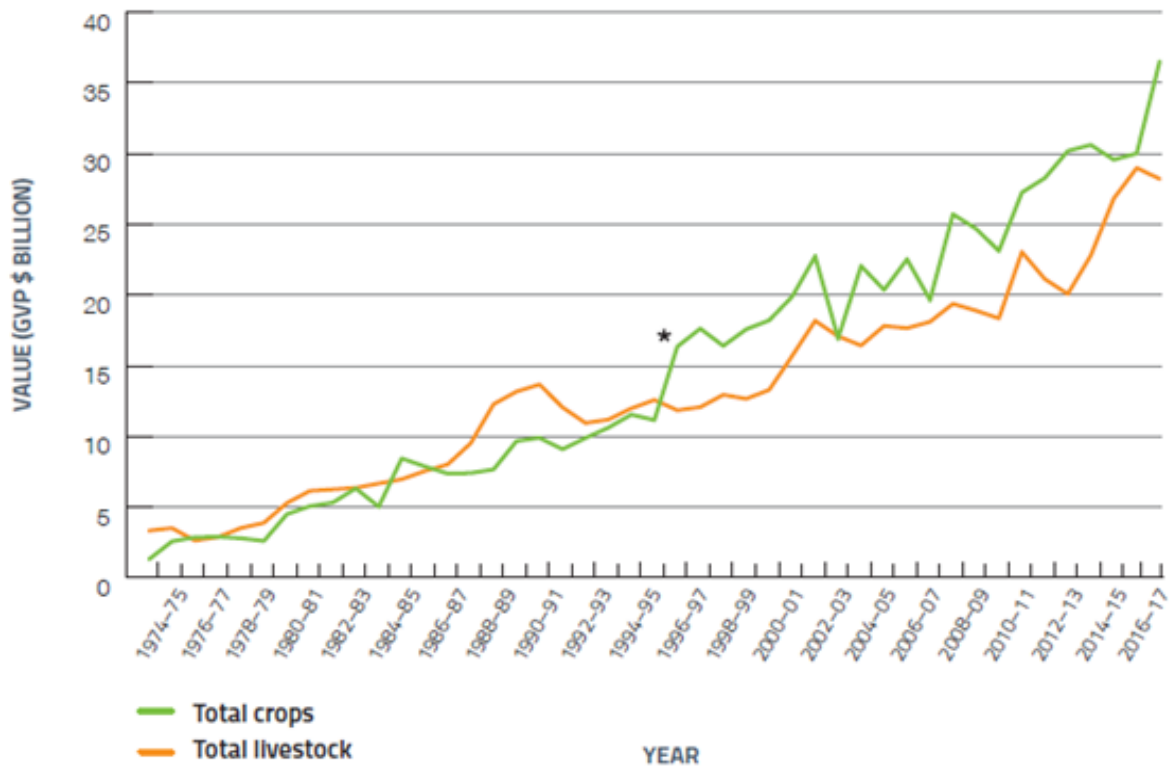
Figure 1-5. Gross value of plant and animal production industries in Australia from 1972 to 2017 (from National Plant Biosecurity Status Report, 2017).

According to the Australian Bureau of Agricultural and Resource Economics (2016–2017), plant production industries had a gross value of $36.5 billion, which is higher than the value of livestock production industries, a situation that has existed for a decade (Figure 1-5). Thus, it can be seen that plant production makes a significant contribution to the Australian economy with an increasing amount of produce, particularly grains, cotton and higher value premium horticultural crops, being exported overseas. These statuses indicated that plant biosecurity is essential to Australia (Australian Bureau of Statistics, 2017).

1.1.3.3 Biological invasion in Australia

Produce destined for overseas markets must meet the standards set for market access, which often includes providing evidence that production areas are free from certain pests. Production and trade could be jeopardized by an incursion of a new pest into fields, orchards and plantations (Wan *et al*. 2017). Australia is fortunate to be free from many serious plant pests that exist overseas, due to its geographic isolation, however, with increasing international trade, movements of shipments, planes and tourism the risk of new IAS arriving is increasing (National Plant Biosecurity Status Report, 2017). This may result in more pressure than ever on Australia's biosecurity prevention and management of exotic pests.

Based on the analysis of the records in Invasive Species Compendium from CABI (http://www. cabi.org/isc), currently, there are 910 invasive species in Australia. The number of weeds species is the largest, which accounts for 40% of the total species, followed by plant pests with 147 species (16.2%). Additionally, a total of 86 species of invasive fungi, bacteria, virus, and parasitic nematodes of plants were recorded (Figures 1-6 and 1-7).
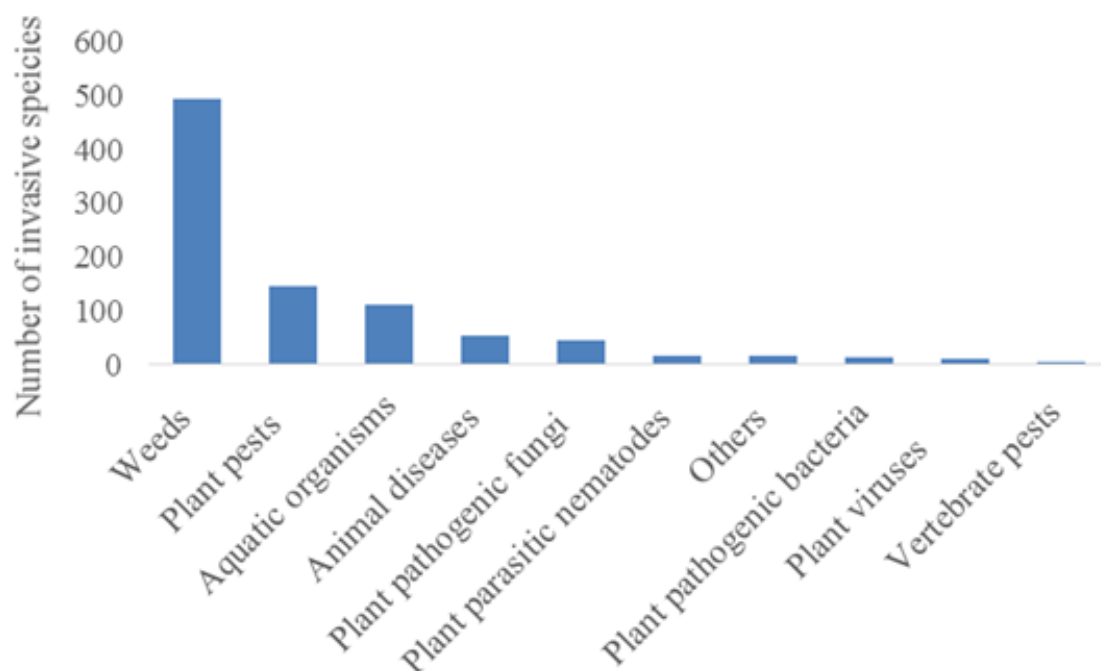
Figure 1-6. Numbers of various categories of invasive alien species in Australia.

IAS have invaded almost all the habitats of Australia, including terrestrial (managed/semi-natural), littoral, inland waters, and oceans and so on. Among that, most invasive species can be found in the terrestrial (Figure 1-8), where there are more frequent human activities, and

they have especially flourished in the habitats that are mostly disturbed by human activities (Figure 1-9). Coming in second is littoral where 255 invasive species can be found (Figure 1-8).
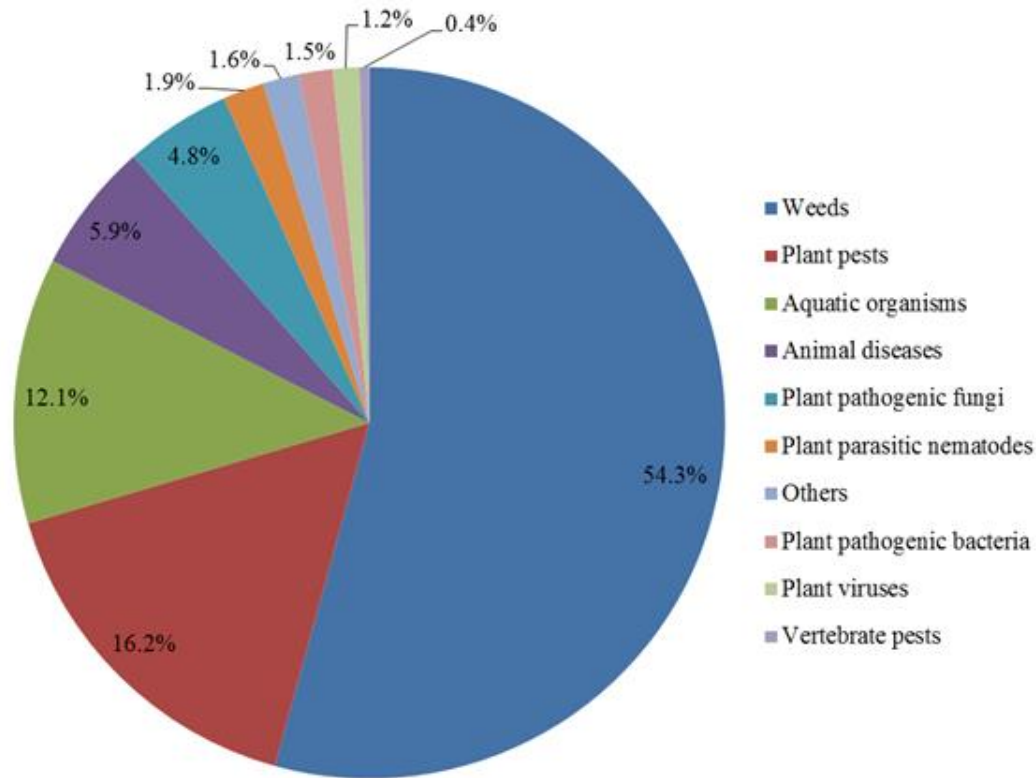
Figure 1-7. Percentages of various categories of invasive alien species in Australia.

In addition, there is a total of 189 invasive species occurring in water areas, of which 82 invasive species occur in freshwater, 64 in brackish, and 53 in marine (Figure 1-8). More remarkable is the fact that of the 430 species that invade terrestrial ecosystems, 300 species are invading agricultural ecosystems (Figure 1-8), suggesting agricultural ecosystems are suffering from severe invasion of alien species, and agricultural biosecurity has become a serious environmental issue. More than 500 invasive species are found in Queensland, followed by New South Wales with 459 species, and third is Victoria with 346 species. It shows that the distribution pattern of IAS shows a clear correlation with ecological environment, agricultural development, and external trade (Figure 1-9) (National Plant Biosecurity Status Report, 2017).
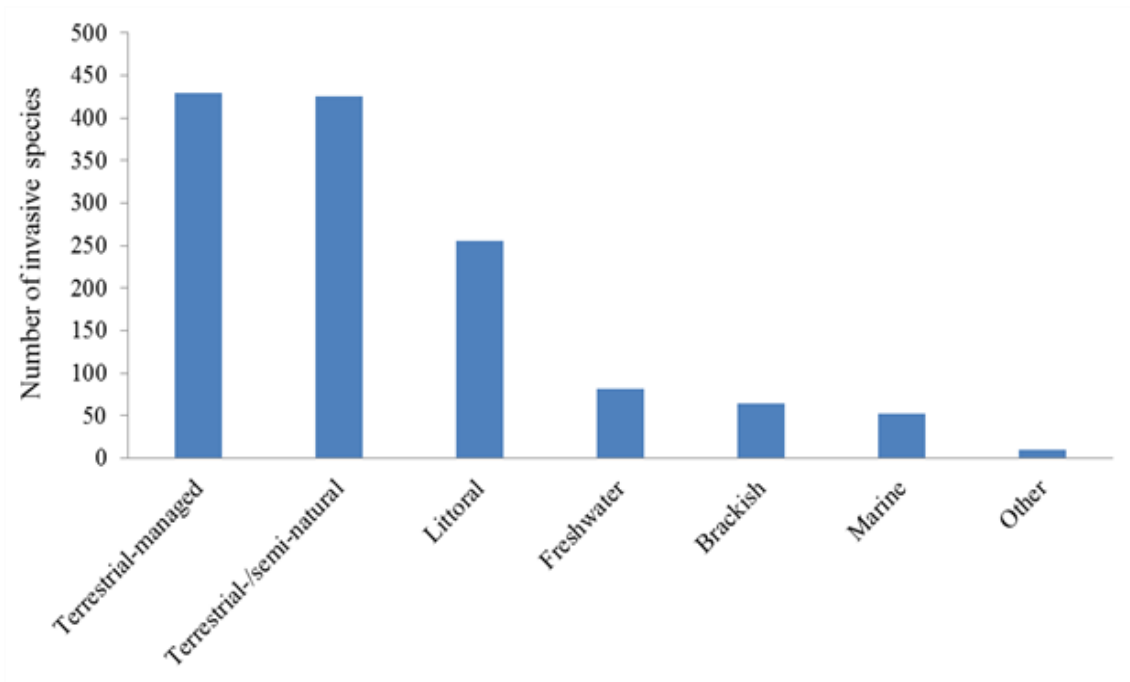
Figure 1-8. Numbers of invasive alien species in each habitat in Australia.
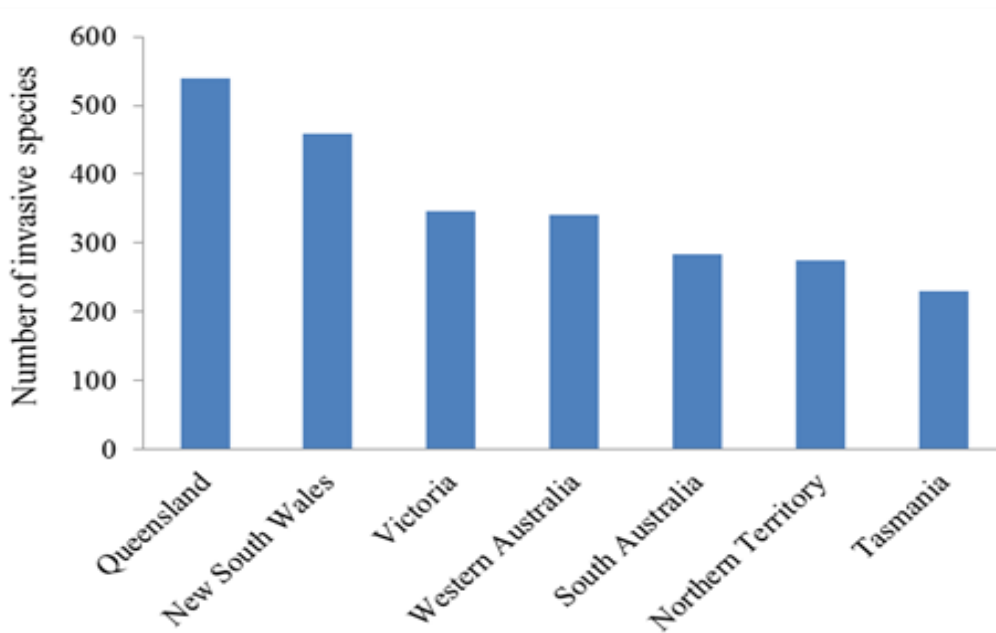
Figure 1-9. Numbers of invasive alien species in each state in Australia.

Introduction and dispersal are the important processes of biological invasion, which it is the basis of colonization and outbreak of invasive species (National Plant Biosecurity Status Report, 2017). In Australia, there are many pathways or vectors involved in the introduction

and dispersal of IAS, among that, 259 alien species depend on water for introduction and dispersal, which may be related with the geographical location of Australia being surrounded by water, and the second is the soil, sand, and gravel with 186 species, followed by land vehicles with 160 species (National Plant Biosecurity Status Report, 2017). Additionally, shipping is the main method for Australia to trade with other countries and regions, thus the ballast water (36 species) is also one of major invasion pathways in Australia (Figure 1-10) (National Plant Biosecurity Status Report, 2017).
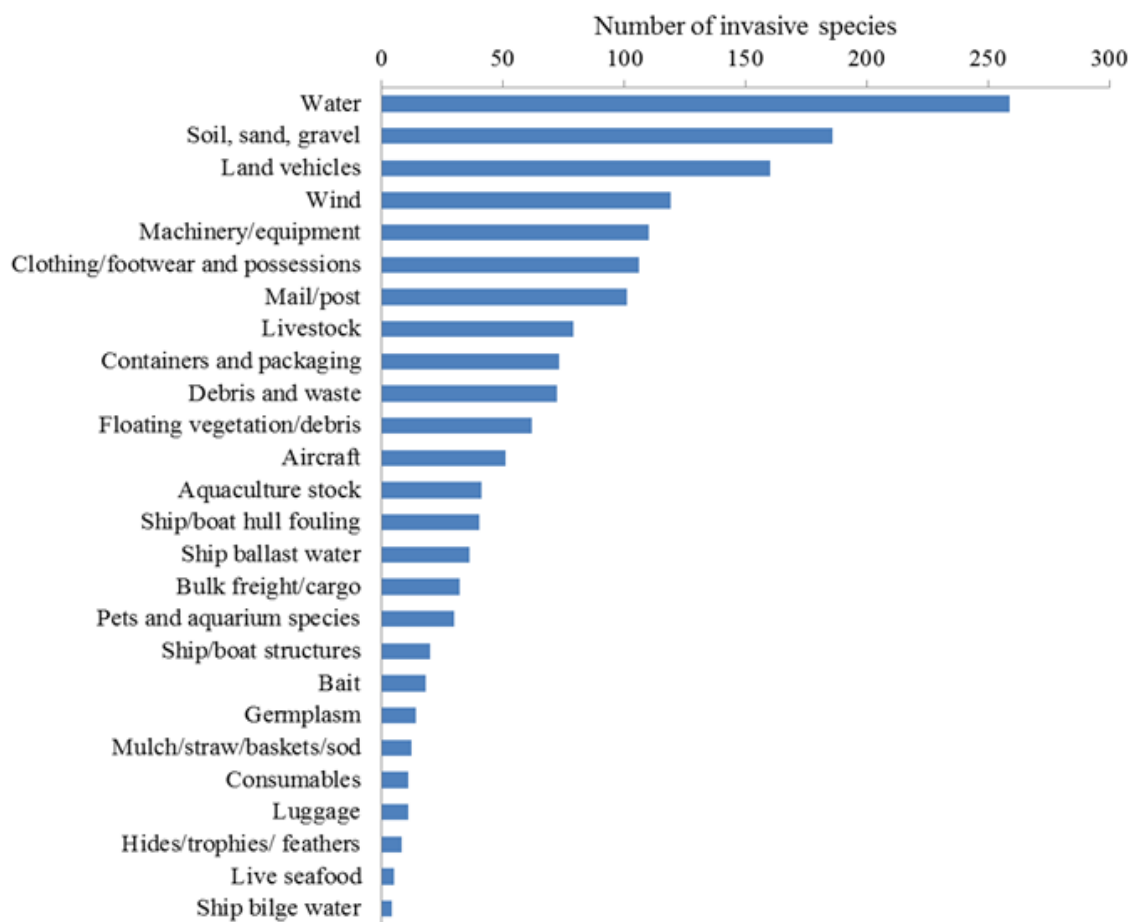
Figure 1-10. Numbers of alien species introduced and dispersed by different pathways and vectors in Australia.

1.1.3.4 Biosecurity in Australia

1.1.3.4.1 Biosecurity status in Australia

Australia's biosecurity system is a collaborative effort between federal and state governments and industry, which played a critical role in reducing risk and shaping it to become one of the few countries in the world to remain free from the world's most severe pests and diseases. While geographical isolation of Australia has played a key role in maintaining this status, the isolation as an island nation is rapidly changing as the barriers of time and distance become less relevant and international travel and trade increase. With the enormous length of Australia coastline which produced a variety of pathways for invasive alien pests and diseases to enter. In order to mitigate and control this situation a variety of methods have been employed according to Department of Agriculture and Water Resources, x–ray machines, surveillance, and inspection of, parcels, luggage, shipments, animals, plants and cargo containers entering Australia and the most effective and efficient, the instantly recognizable detector dogs.

Australia currently aligns biosecurity across the continuum from offshore to border to onshore (Plant Health Australia, 2013). The department employs a range of technology and methods, including research, shared global information and intelligence, to safe guard against the introduction and spread of IAS (Black and Bartlett 2020). Surveillance and monitoring are also essential in high risk areas combined with border control activities, which together aim to detect and manage potential biosecurity threats at airports, seaports, and international mail centres (Black and Bartlett 2020).

In 2015, the Australian Biosecurity Act was enacted, which explains how the country manages biosecurity threats to plant, animal and human health (National Plant Biosecurity Status Report, 2017). The strict biosecurity control protocols protecting Australia borders have effectively decreased the chance of IAS entering into Australia, protected its unique ecosystem, wildlife population, native flora and fauna, and most importantly protected the $32 billion agriculture trading industry (Australian Bureau of Statistics, 2017).

1.1.3.4.2 Plant biosecurity in Australia

Australia is fortunate to be free from many serious plant pests that exist overseas, due to its geographic isolation and more than a century of effective quarantine measures. The enviable plant health status confers significant benefits (Black and Bartlett 2020). Not only does it

protect the unique natural environment, but it also supports the rural way of life and the economy. It allows higher yields for farmers, with less pesticide usage, resulting in lower production costs and greater acceptance of the produce around the world. To maintain this favourable situation, Australia places a high priority on plant biosecurity, a necessity in this age of increased global trade and travel. Firstly, Plant Health Australia (PHA) has been established, which applied for assessments of pest threats industry by industry to develop a list of high priority pests that warrant special biosecurity efforts. Each of the 370 species on the list would thrive in Australian conditions, with the potential to cause ongoing damage to native flora and plant production systems.

(1) Emergency plant pest responses

For agricultural industries and producers, the Australian government has issued the following documents - "Australian Emergency Plant Pest Response Plan" and "Government and Plant Industry Cost Sharing Deed in Respect of Emergency Plant Pest Responses" to deal with the agricultural industry economic losses related to the emergency plant pest and biological invasions, and cost sharing between governmental and plant industry (planthealthaustralia.com.au). These policies have guaranteed the industries and producers' sustainability and will stimulate their efforts to control and manage the risks and threats from plant pests and biological invasions in their own business (Plant Health Australia, 2013).

(2) Pest risk assessment and management

Risk assessment is a process to evaluate the risk that a species will be transported and introduced, establish, increase in abundance, spread and cause impacts. Risk assessment posed by plant pests and exotic pests listed in Industry Biosecurity Plans (IBPs) considers relevant international standards on risk assessment developed under the International Plant Protection Convention (IPPC) (FAO, 2013).

The risk assessment includes entry potential, potential economic impact and risk potentials and impacts. IBP worked out a standard for plant risk assessment (Plant Health Australia, 2013). In addition, for better understanding of the risks, a matrix of the combined likelihood rating and economic consequence rating has been given for users' references (Table 1-1).

Table 1-1. Economic consequence rating with combined likelihood rating.

		Combined likelihood rating				
		High	Medium	Low	Extremely low	Negligible
Economic consequence rating	Extreme	Extreme risk	Extreme risk	High risk	Medium risk	Low risk
	High	High risk	High risk	Medium risk	Low risk	Very low risk
	Medium	Medium risk	Medium risk	Low risk	Very low risk	Negligible risk
	Low	Low risk	Low risk	Very low risk	Negligible risk	Negligible risk
	Very low	Very low risk	Very low risk	Negligible risk	Negligible risk	Negligible risk
	Negligible	Negligible risk	Negligible risk	Negligible risk	Negligible risk	Negligible risk

1.2 Risk analysis and bio-economics of IAS to inform policy and management

The risk to agriculture industries is undoubtedly inherent and ubiquitous, causing huge consequences to consumers and stakeholders. Risks cut off supply chains, causing massive financial and economic losses (Australian Bureau of Statistics, 2017). Agricultural risks are also the main reason for short term food insecurity, creating a vicious cycle in the developing world, trapping millions of families in shock and recovery (World Bank, 2016). Effective agricultural risk management (ARM) is essential in reducing poverty, increasing economic growth, and improve food security. Pests are one of the most significant production risks, especially for food crops, and sometimes may be exacerbated by adverse weather events, which have significant impacts both on the economy and on food security. The damaging impact of pests are influenced by domestic agricultural practices to a great degree (Lodge *et al*. 2016).

1.2.1 Risk assessment and management of IAS

Protecting plant resources from pests especially the insects, diseases and weeds which can spread internationally is a major challenge for plant protection organisations. It is important to know the value of risk impacts in order to estimate the benefits from investing in risk management. Government policy makers have received advice and support from national economists and scientists whom together contributed their knowledge and experience, also taking into account the stakeholders' opinions when developing policy and regulations to alleviate IAS risks (MacLeod *et al.* 2015).

IPPC, the international standard-setting body for plants defined risk analysis into three independent yet unified aspects, risk assessment, risk management and risk communication (FAO 2007, 2013). Risk assessment and risk management are interacting, but functionally separate, risk analysis activities. Risk assessment characterizes the likelihood and severity of potential adverse effects of exposure to hazardous agents or activities. Risk management is the process of identifying, evaluating, selecting, and implementing actions to reduce risk. There may be no sharp boundary between risk assessment and risk management in some analytic elements, e.g. the identification and evaluation of risk reduction measures. Risk managers are distinguished, however, as those with authority to make decisions and take actions to lessen or eliminate risk (National Research Council, 1996).

Biological invasions process through four stages and provide management opportunities at each stage including introduction, establishment, spread, and impact. Recent scientific progress has modified estimates of probability and associated uncertainty. Scientific progresses came from species-specific trait-based risk assessments on introduction, establishment, spread, and impact pprobabilities, particularly pathways of species attached commercial trade, transportation pathways, introduction and spread, of spatially explicit dispersal models, and species distribution models (Lodge *et al.* 2016).

Conceptualizing the invasion process in this way highlights that preventing invasions requires management of pathways at the beginning of the invasion process and that reducing harm during later invasion stages is more difficult and expensive (Figure 1-11). Although considering the entire sequence of transitions is appropriate for a pathway or for a species that has not yet been introduced, this conceptualization also emphasizes that a risk assessment (RA) can begin at any stage of invasion and may consider all subsequent probabilities to help identify

which management interventions are most appropriate at a given stage of invasion (Lodge *et al*. 2016). A risk analysis approach provides a framework for considering the benefits and harms of both the pathway and any management actions under consideration, the US Environmental Protection Agency developed a framework for using three main steps: a) problem formulation; b) analysis of exposure and effects and c) risk characterization (US EPA, 1998).

Damages per invasive species are extremely high relative to the benefits per species in trade. Risk assessment tools at current levels of accuracy are thus enough to produce economic benefits - in addition to the obvious environmental benefits - for an importing region or nation.
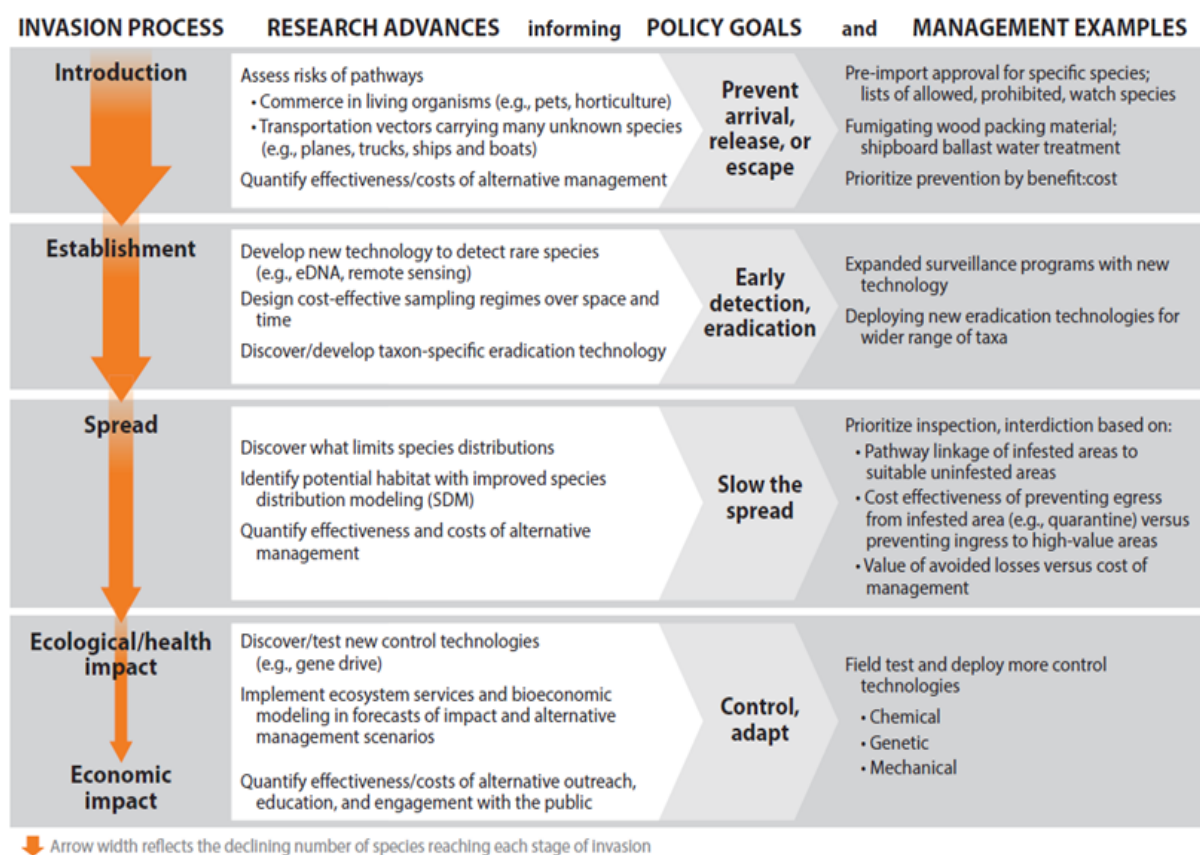
Figure 1-11. Conceptualizing invasions as a process (left column) that includes multiple steps involving human behaviour and the biology of other species helps to identify research priorities (second column), policy goals (third column), and management interventions (right column) that are most relevant to each step in the invasion process (Lodge *et al*. 2016).

1.2.2 Economic Impact Assessment of IAS Risk Analysis

1.2.2.1 Approaches and methods for pest risk analysis

A science-based pest risk analysis (PRA) provides the rationale for determining appropriate plant health regulation for a specified PRA area. Economic impact assessment plays a key role within the PRA process. The International Standard for Phytosanitary Measures (ISPM) 11 states that "Pest risk assessment needs to be only as complex as is technically justified by the circumstances" (FAO, 2004). This rule is critical because it gives the risk analyst the freedom to choose the complexity level of his assessment according to the level of uncertainty and the available resources.

Economic impact assessments are usually made using a qualitative approach (EPPO, 2011; EFSA, 2010). The qualitative approach is following a decision support scheme according to ISPM 11 developed by the International Plant Protection Convention (IPPC) (EPPO, 2011).

Although this qualitative approach, based on classification, is helpful to classify impacts, the status of the outcome is quantitatively not well defined. It has therefore some shortcomings in justifying measures and entails weakness in case of trade disputes. There is a growing awareness that quantitative economic impact assessment is essential to provide a better transparency and objectivity of the quarantine regulation (Sanford 2002).

Conducting quantitative economic impact assessment with the aim of supporting a decision on pest quarantine status or management measures requires subject specific information in terms of data and models. The main quantitative methods that may be used for estimating the economic impact of pest invasions includes partial budgeting, partial equilibrium modelling and computable general equilibrium modelling (FAO, 2007).

Partial Budgeting (PB) is a basic method designed to evaluate the economic consequences of minor adjustments in a farming business. The method is based on the principle that a small change in the organization of a farm business will reduce some costs and revenues, but at the same time add others. The net economic effect of a change will be the sum of the positive economic effects minus the sum of the negative effects (Table 1-1). Due to the marginal approach, PB is not designed to show the profit or the loss of a farm, but the net increase or decrease in farm income (FAO, 2013).

Partial Equilibrium Modelling (PE) is a powerful tool to evaluate the welfare effects on participants in a market which is affected by a shock like a policy intervention or an introduction of a pest. The approach is based on defining functional relationships for supply and demand for the commodity of interest to determine the market equilibrium or, in other words, the combination of prices and quantities that maximizes social welfare (Mas-Colell 1995).

The technique of Input - Output Analysis (I-O) analysis focuses on the interdependencies of sectors in an economy (regional or national), making it suitable to predict an economy-wide impact of changes within a particular sector (Leontief 1986). Central to an I-O analysis is the specification of an I-O table to describe the monetary flows of inputs and outputs among the productive sectors of an economy (Miller and Blair 1985). In an I-O table, economic sectors are aggregated into representative groups. Each sector-group is represented by a row and a column. The rows of the table specify the distribution of total output of a specific sector sold to other sectors (i.e. to intermediate demand) or to final demand (e.g. to final consumption, investments and exports). The columns refer to the production side of a given sector, by denoting the value of inputs of each sector required to produce output.

The Computable General Equilibrium Modelling (CGE) approach combines the strengths of I-O analyses and PE models to answer a wide range of questions. It uses I-O tables to represent the entire economy with the inclusion of functional relationships between actors in this economy as in a PE model. The basic structure of a CGE model can be described in terms of "blocks" of equations that specify demand relationships, production technologies, relationships between domestic and imported goods, prices, household income and numerous equilibrium conditions (Soliman, 2012).

To perform a quantitative economic impact assessment, a calculation framework is required to integrate information on assets at risk with information on the potential area of establishment, the spread, the potential damage, and the economic consequences to producers, consumers, and import and export. Soliman (2012) developed a generic bio-economic framework for assessing economic impacts that contains the following modules (Figure 1-12): (1) a climate module describing the climate suitability for the pest species, (2) a host module describing the spatial distribution of the hosts, (3) a spread module predicting the potential spread of invasive species, (4) a climate based host damage function and (5) an economic impact module defining the

models to determine producer and market level impacts. To develop this framework, the risk analyst will need input data and economic models.

1) Climate module
The suitability of the environment to damage expression of host crops

2) Host module
Distribution of the host crops over space

3) Spread module
How the pest spreads, and builds up its population over time and space

4) Climate based host damage function
A relationship between the climate layer, and the likely level of yield or quality loss

5) Economic module
Direct impact at the producer level and indirect impact at the market level

Figure 1-12. Bio-economic framework to assess the economic impacts using a quantitative approach (Soliman, 2012).

1.2.2.2 Process and model selection of economic impact assessment in PRA

On conducting an economic impact assessment, the risk analyst must make choices regarding to the most appropriate technique to apply (Figure 1-13). The appropriate technique will provide an acceptable estimate of the economic impacts while minimising uncertainty with respect to conclusion. In addition, the technique should use the minimum possible resources in terms of data, skills and time (Soliman, 2012).
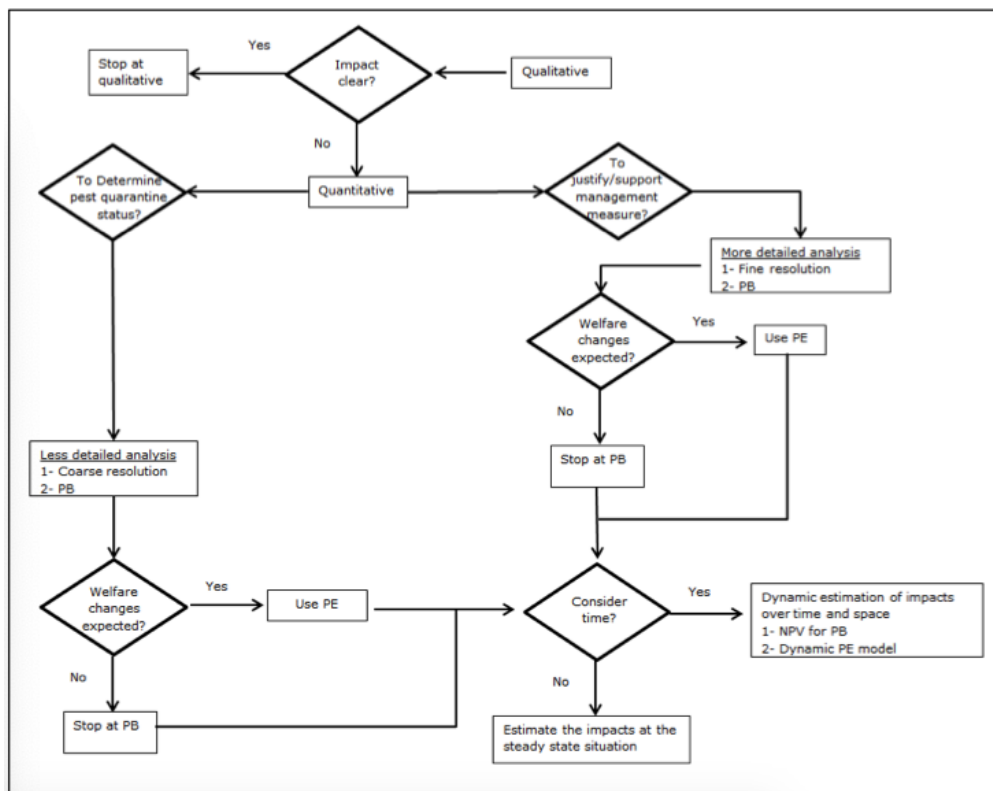
Figure 1-13. Guidance scheme for choosing the most appropriate technique for economic impact assessment (Soliman, 2012).

The first step in selecting the most appropriate technique is to decide on the need of a quantitative approach. Generally, the qualitative approach is the default method to use. A quantitative approach is subsequently recommended when the qualitative approach does not give a clear indication of the importance of the potential economic impacts or when a metric estimation of the impacts is needed to justify or to support a management measure. Quantitative impact assessment can be conducted at various levels of complexity (i.e. less or more detailed analysis). Choosing the most appropriate output resolution of the economic model will depend on pest characteristics.

The development of the pest risk analysis science has been marked by a series of debates about the nature of plant health regulation and the methodologies that are appropriate for its study. In recent years, this debate has centred upon the relative merits of qualitative and quantitative methods to assess pest risk and impacts (EFSA, 2010). The overall lack of consensus among researchers is illustrated by the range of views expressed about the strengths and weaknesses of the qualitative and quantitative research methods (Table 1-2).

Table 1-2. Strengths and weaknesses of the quantitative and qualitative approaches
(Soliman 2012).

	Quantitative		Qualitative	
	Strengths	**Weaknesses**	**Strengths**	**Weaknesses**
Usage	More adequate to apply when the risk is ambiguous	High resource requirement (in terms of data, time and skills)	• More adequate to apply when the risk is clear beforehand • Low resource requirement (in terms of data, time and skills)	The possibility of being misused for political reasons
Transparency	Transparent and objective	Complexity of the underlying economic and spread models	Straightforward assessment procedure	Less transparent than quantitative approach
Impact estimation	Provides a (metric) evaluation of the impacts	It is not verified whether it can provide more accurate results (closer to the true value) than qualitative approach	Make the best use of the expertise, caution and wisdom of the PRA experts	Impacts could be overlooked (as it is hard to capture the indirect impact qualitatively, e.g. price changes.)

PRAs are heavily reliant on a range of evidences, many of them are qualitative and therefore may not be appropriate for quantification. By adapting a valid conceptual framework that applies relevant qualitative and quantitative methods that support each other, we will be able to achieve a sound prediction of the pest economic impacts. A quantitative approach is preferable if the expected economic impact is ambiguous when using a qualitative approach, and when there are sufficient resources to conduct the analysis (EFSA, 2010).

1.2.2.3 The role of bio-economic analyses in IAS management

Bio-economic analyses exhibit application in risk management programs by covering an extensive length of time horizon, that can accelerate overall performance of ecosystem services and human welfare, because invasion of harmful non indigenous species are prevented while trading of benign species continue (Keller *et al.* 2007).Risk analysis method has optimized the estimation of all transition probabilities and related uncertainties participated in biological invasions and has advanced bio-economic analyses of the cost and benefit of substitute management methods (Peters and Lodge 2009).Invasive alien species requires multi-

jurisdictional management a challenging yet essential collaboration for bio-economic research and application (Peters and Lodge 2009).

Bio-economic models are responsible for interacting dynamic scenarios with ecological and economic systems and provide policy makers a clear view of economic consequences of alternative management strategies (Soliman 2012). In summary, through extensive research and modelling indicated prevention is the most efficient long-term strategy.

1.3 Overview of specific invasive pests threatening Australia

Statement of Declaration

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By signing the statement of contribution, each author certifies that:
- ➢ The candidate's stated contribution to the publication is accurate (as detailed above).
- ➢ Permission is granted for the candidate to include the publication in the thesis
- ➢ The sum of all co-author contributions is equal to 100% less the candidate's stated Contribution

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Contribution to the Paper	Structure format, revision, supervision
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Signature	**Date** 04/11/2020

1.3.1 Fall armyworm invasion in Australia

Invasive alien species (IAS) seriously threaten agricultural and forestry ecosystems, biodiversity, human health, and cause significant economic losses. The emergence and invasion of IAS are closely linked with increasing trade and have become a major global issue. It is vital to effectively manage IAS (Wan and Yang 2016).

Fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is native to tropical and sub-tropical areas of the Americas (Sparks 1979). FAW has a strong migration ability and in the past three years it has invaded 47 African countries, 18 Asian countries and now Australia where it seriously threatens crop production (https://www.cabi.org/isc/datasheet/29810). FAW is polyphagous and two sympatric host-plant strains have been identified, the "corn-strain" (C-strain) feeding mostly on maize, cotton and sorghum and the "rice-strain" (R-strain) mostly associated with rice and various pasture grasses (Nagoshi and Meagher 2004). In the past few decades, FAW has developed multiple resistance and cross-resistance mechanisms against various kinds of insecticides and transgenic Bacillus thuringiensis (Bt) maize, due to the extensive use of the treatments to manage the pest. The synthesis of these biological characteristics has contributed to its spread and invasion, and increased its economic importance. The cost of controlling FAW is enormous: according to statistics from the Food and Agriculture Organization (FAO), Brazil alone spends US$600 million each year in attempts to control FAW (Wild 2017). Due to its perniciousness and invasiveness, it was rated as one of the top ten out of 1 187 arthropod pests by the Centre for Agriculture and Biosciences International (CABI) in the report "State of the World's Plants" in 2017 (Wild 2017).

1.3.1.1 Fall armyworm biology and ecology

IAS are superior in terms of their life cycle, genetics and evolution when compared with related non-invasive species. These characteristics are embodied in the morphology, physiology, ecology, genetics and behaviour of the species. It is presumed that FAW invasiveness is associated with its superior biological characteristics including absence of diapause, short generation time, high fecundity, high polyphagy, long-distance migration ability and formidable resistance to insecticides, viruses and Bt toxin.

1.3.1.1.1 Absence of diapause, short generation time and high fecundity

FAW is a lepidopteran insect that undergoes holometabolous metamorphosis. Its life cycle includes egg (2–3 days), larvae (total six instars, 13–14 days), pupae (7–8 days) and adults (7–21 days). FAW has a generation time of approximately 30–40 days during the warm summer months (daily temperature of ~28ºC), and approximately 55 days in cooler temperatures (Prasanna *et al.* 2018; Sharanabasappa *et al.* 2018). It does not have the ability to diapause, so the number of generations occurring in an endemic area depends on environmental conditions, e.g., temperatures and host plants (Prasanna *et al*. 2018). In several regions of North America, FAW occurs seasonally through migration and it dies out in cold winter months. Whereas in the invaded countries, such as most of Africa, it occurs throughout the year with overlapping generations wherever host plants are available and climatic conditions are favourable (Abrahams *et al*. 2017). In southern China, it has been reported that FAW occurred all year round in the winter corn fields without diapause in winter (Qi *et al*. 2020), however, it could not survive when the average temperature was below 10°C for 8–10 days in Anhui Province (Xie *et al*. 2020). Average egg production per female is about 1 500 (a maximum of over 2 000) in Africa, demonstrating high fecundity (Prasanna *et al*. 2018). However, the egg production in India (1 064 eggs per female) and China (1 052–1 323 eggs per female when feeding on different maize varieties) are lower than that in Africa (Prasanna *et al*. 2018; Sun *et al*. 2020). Fecundity appears to be affected by variations in biotic (different hosts) and abiotic (temperature, humidity, etc.) factors.

1.3.1.1.2 Highly polyphagous

FAW has a wide host range of more than 353 recorded plants from 76 families, principally Poaceae (106), Asteraceae (31) and Fabaceae (31). Among them, it has strong preference for maize, rice, sorghum, cotton, pasture grasses and sugarcane (Montezano *et al*. 2018; Dumas *et al*. 2015), which are all major cultivated crops in America, Africa and Asia. Remarkably, FAW has developed two defined strains, C-strain and R-strain, which are morphologically identical but differ in host range (Groot *et al*. 2010), mating behaviors (Schofl *et al*. 2009), genetics (Dumas *et al*. 2015) and pheromone components (Groot *et al*. 2010) in natural and laboratory maintained populations (Velasquez-Velez *et al*. 2011; Dumas *et al*. 2015). The asymmetric distribution of the two strains with selective plant host preference is consistently observed. The C-strain feeds predominantly on maize, cotton, and sorghum while the R-strain feeds primarily on rice and pasture grasses (Dumas *et al.* 2015). However, in Nagoshi *et al.* (2014), a small number of individuals of one strain were found in host habitats dominated by the other strain.

In addition, previous laboratory studies indicated that both strains can exploit preferred hosts of the other strain, suggesting that host preference observed in the field cannot fully be explained by differential larval feeding (Groot *et al.* 2010). In addition, strain-specific female oviposition associated with host-preference has been observed under laboratory conditions (Hay-Roe *et al.* 2011).

1.3.1.1.3 Long distance migration ability

FAW displays high migratory ability (over 100 km per night), through which the moths can find a broad range of habitats within its preferred environmental conditions (Tendeng *et al.* 2019). Laboratory testing has shown that 3-day-old moths have the strongest flight capacity and average flight distance, flight duration and flight velocity in 24 h can be 29.21 km, 11.00 h and 2.69 km h–1, respectively (Ge *et al.* 2019). In its native region, FAW populations can only overwinter in southern Texas and southern Florida, which are considered the northern-most winter- breeding areas available. However, in late summer, FAW are annually detected as far north as Ontario and Québec, Canada, which are considered to be migratory populations (Westbrook *et al.* 2016). The ability to migrate long distances has been confirmed by radar monitoring of noctuid moth species (including FAW) in Texas which identified a 400-km migratory flight displacement in 7.8 h (Westbrook 2008). In addition, in the Caribbean, the FAW can migrate from Puerto Rico to Barbados, a distance of more than 900 km (Nagoshi *et al.* 2017). In its invaded region in Africa and Asia, the spread of FAW also depends on its formidable flight capacity.

In China, FAW quickly invaded almost all maize belts within a year (Jiang *et al.* 2019). There are two main migratory routes for spread and reinvasion in China, the western and eastern routes. The origin of the western route is the westerly winter-breeding region (Myanmar/Yunnan, China) via Guizhou and Sichuan provinces through windborne transport. The origin of the eastern route is the easterly winter-breeding region (northern Thailand, Laos, Vietnam and Guangxi and Guangdong, China) via east-central China before arriving in the main maize belts (the Huang-Huai-Hai and Northeast Regions) with the help of Asian monsoons (Li *et al.* 2020).

1.3.1.1.4 Formidable adaptability to adversity

FAW has developed high resistance to a range of insecticides. In the mid-1980s, it developed resistance to carbaryl, methyl parathion, trichlorfon and diazinon in the southeastern United States (Pitre 1986). Subsequently, it developed more than 200-fold resistance to organophosphates and carbamate successively in North, Central and South Florida (Yu 1991). In 2002, two field FAW populations in Citra and Gainesville, Florida showed high resistance to carbaryl (626- and 1 159-fold), and moderate resistance to parathion-methyl (30- and 39-fold) (Yu and McCord 2007). In 2016, resistance ratios (RR) of various FAW populations from Mexico and Puerto Rico to chlorpyrifos, permethrin, flubendiamide, and chlorantraniliprole were up to 500-fold; RR to methomyl, cypermethrin and deltamethrin were 20- to 48-fold; and RR to ethyl dodecycin, dodecycin, emamectinbenzoate and abamectin were 7- to 14-fold (Gutierrez- Moreno *et al.* 2019). By 2017, FAW had developed resistance to at least 29 insecticides, including carbamates, organophosphorus, pyrethroids and Bt insecticidal proteins in the Americas (https://www.pesticideresistance.org/). Currently, polyfungicide is the preferred pesticide for FAW control in corn fields and is applied three times during a growing season in Brazil. FAW has developed resistance to polyfungicide in Brazil, as well as to cyhalothrin, chlorpyrifos, and guanidine, and transgenic Bt maize Cry1F and Cry1Ab (Li *et al.* 2019). Some studies have shown that the FAW population that invaded China carries resistance to organophosphate and pyrethroid pesticides (Zhang *et al.* 2020).

The transgenic insect resistant Bt maize has also been widely used to control FAW (Buntin *et al.* 2001). When exposed to Bt-maize toxin, FAW can develop monogenic (based on a single gene) or oligogenic (based on a few genes) resistance to these transgenic crop varieties (Huang *et al.* 2014). For example, Cry1F resistance in FAW has been detected in maize fields from Puerto Rico (Storer *et al.* 2010), southeastern mainland USA (Huang *et al.* 2014), Brazil (Farias et al. 2014), and Argentina (Chandrasena *et al.* 2018). Furthermore, it has developed resistance to other Bt proteins including Cry1Ac, Cry1Ab and Cry1A.105 (Storer *et al.* 2010).

Baculoviruses, the biological control agent, are widely used to control lepidopteran pests, and offers a promising alternative to chemical pesticides to avoid insecticidal resistance. However, several studies have now shown that FAW has developed resistance to the *S. frugiperda* multiple nucleopolyhedrovirus (SfMNPV) and Autographa californica multiple nucleopolyhedrovirus (AcMNPV) (Martinez *et al.* 2004; Haas-Stapleton *et al.* 2005).

1.3.1.2 Fall armyworm outbreak and damages

In the past two centuries, the distribution of FAW was limited to tropical and sub-tropical areas in the Americas, with several outbreaks at irregular intervals (Sparks 1979). However, in recent years, it has successfully invaded into Africa and Asia, and is in the process of invading Oceania (Figure 1-14).

FAW was first detected in West and Central Africa in January 2016, and spread to the islands of São Tomé and Príncipe within 2 months (Goergen *et al.* 2016), followed by sudden outbreaks in 46 African countries including many countries in central, eastern and southern Africa (Figure 1-14) (https://www.cabi.org/isc/datasheet/29810). Molecular identification of FAW showed that the invasive population in Africa includes both C-strain and R-strain (Assefa 2019). The invasion into India was first reported in May 2018 (Mahadevaswamy *et al*. 2018; Sharanabasappa *et al*. 2018), and then quickly spread to Sri Lanka, Thailand, Yemen, Nepal, Myanmar and Bangladesh (Farmer 2019).

Genetic diversity studies showed that the FAW population in India belongs to R-strain based on polymorphisms in the cytochrome oxidase subunit I (COI) gene (Mahadevaswamy *et al.* 2018) and triose-phosphate isomerase (Tpi). These findings suggest a small, shared founder population as the source of FAW in Africa and India (Nagoshi *et al*. 2019). FAW invaded Yunnan, China in December 2018 (Sun *et al*. 2021), spread rapidly and subsequently outbreaks were detected in 26 provinces (autonomous regions, municipalities) (Jiang *et al*. 2019). Both COI and Tpi showed that the invading populations in China were C-strain (Zhang *et al*. 2019). According to reports from the European and Mediterranean Plant Protection Organization (EPPO), FAW was first found in January 2020 on the islands of Saibai and Erub, in the Torres Strait and then at Bamaga, in the northern Queensland, Australia. By May of 2020, it had spread to 11 regions of Queensland, three regions of the Northern Territory, and three regions of Western Australia (https://gd.eppo.int/taxon/LAPHFR/distribution). In addition, Timor-Leste and Mauritania have also confirmed FAW in 2020 (http://www.fao.org/fall-armyworm/monitoring-tools/ faw-map/en/).

Maize yield losses have been estimated at 15 to 73%when infested with FAW (Hruska and Gould 1997). The annual economic losses in Ghana and Zambia have reached US$177.3 million and US$159.3 million, respectively (Abrahams *et al*. 2017). Collectively, maize, rice, sorghum and sugarcane, have suffered total economic crop losses of US$13 billion per annum

in sub-Saharan Africa (Abrahams *et al*. 2017). Estimation of the potential economic loss of maize in China caused by FAW indicates a range from US$5.4–47 billion per annum (Qin *et al*. 2020).
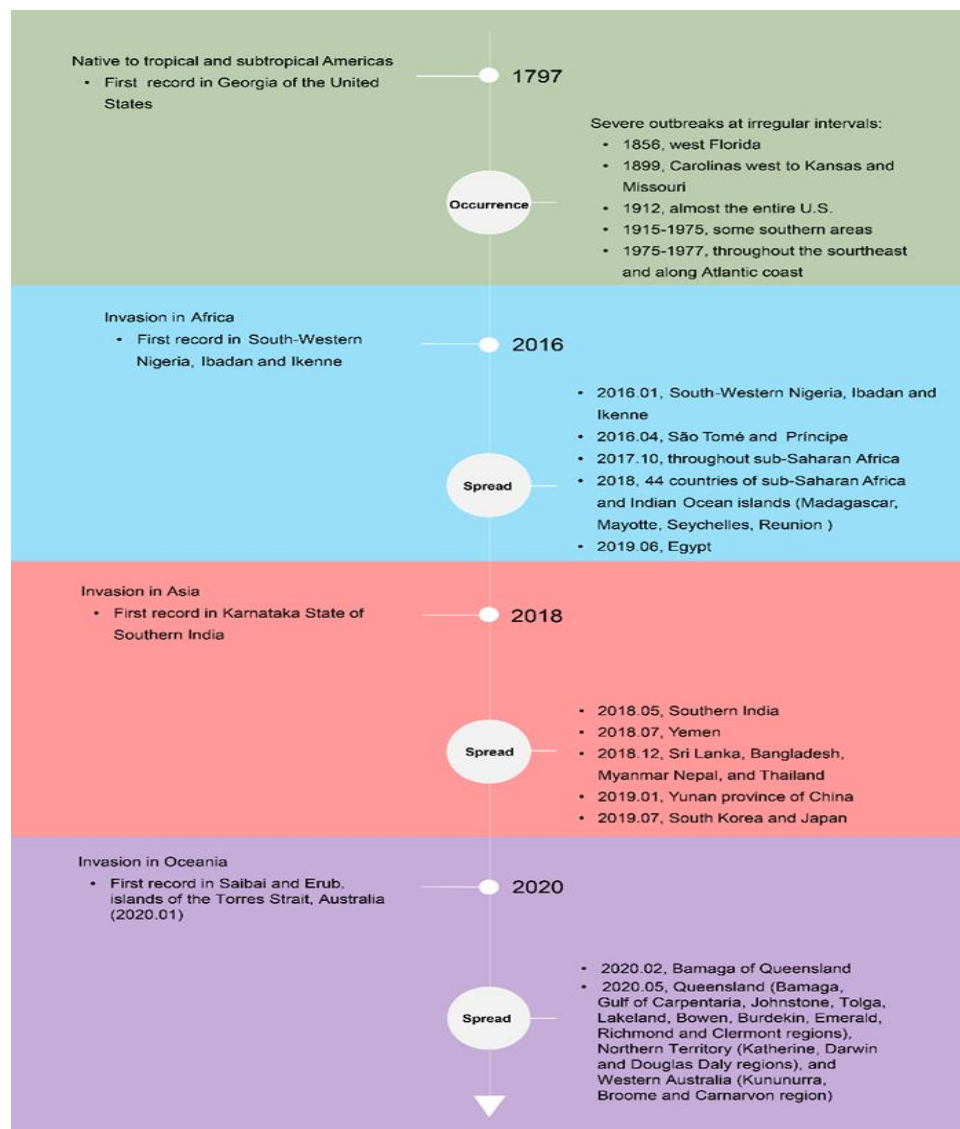
Figure 1-14. Invasion and outbreak of *Spodoptera frugiperda* (fall armyworm) in its native and invaded regions.

1.3.2 Tomato potato psyllid invasion in Australia

The tomato potato psyllid (TPP), *Bactericera cockerelli*, is a psyllid native to North America that has invaded New Zealand in 2006 (Teulon *et al*. 2009) and Western Australia in 2017. The outbreak was first reported in February 2017 in a strawberry farm near north of Perth and due to interstate quarantine protocols all Western Australia strawberries are destroyed with a face value of $80 million Australian dollars (https://www.abc.net.au/news/rural/2017-04-27/strawberry-industry-braces-for-psyllid-hit/8475996).

Bactericera. cockerelli was reported as a major pest in potatoes in 2001 (Butler and Trumble 2012). As its name suggests, TPP feeds on tomato, potato and other Solanaceae crop, where feeding of the nymphs causes a symptom called psyllid yellows, presumed to be the result of a bacterial plant pathogen called *Candidatus* Liberibacter solanacearum (CLso). Studies have shown that the infestation of *Bactericera cockerelli* occurring early in the growing season and on crops with significant leaf canopy in the summer appears to be associated with the maximum potato yield losses. In addition to psyllid yellows caused by *Bactericera cockerelli* feeding, also cause potato tubers to manifest a disease complex called Zebra chip (Munyaneza and Henne 2012), the characteristic of dark stripes caused in potatoes results it to be unmarketable. *Bactericera cockerelli* also led to serious impact on the yields of potatoes and tomatoes in greenhouse worldwide, which resulted in large economic losses (Munyaneza 2010).

Government of Western Australia Department of Agriculture and Food has taken swift action since 2017, efforts were applied to eradicate and manage *Bactericera cockerelli* without further spreading to other regions of Australia. And informing the public on high alert of *Bactericera cockerelli*.

1.3.2.1 Tomato potato psyllid biology and ecology

1.3.2.1.1 Diversity of host plant

Citrus psyllid has a wide range of host plants, including 160 plants from up 20 families (Puketapu 2011; Al-Jabr 1999). For example, *Amaranthaceae, Asclepiadaceae, Asteraceae, Brassicaceae, Chenopodiaceae, Convolvulaceae, Fabaceae, Lamiaceae, Lycophyllaceae, Malvaceae, Menthaceae, Pinaceae, Poaceae, Polygonaceae, Ranunculaceae, Rosaceae, Salicaceae, Scrophulariaceae, Solanaceae*. The main cash crop hosts are potato (*Solanum tuberosum*), tomato (*Lycopersicon esculentum*), pimento (*Capsicum* spp.), sweet potato (*Ipomoea batatas*), eggplant (*Solanum melongena*), and pepper (*Piper nigrum*).

1.3.2.1.2 Developmental period

There are three stages in the life cycle of *Bactericera cockerelli*, including egg, nymph and adult. Eggs can be laid on all parts of the leaf, but are often found on the leaf edge, and attached to the leaf by a short stalk. The nymph consists of five instars with a developmental period of 12 to 25 days. The wing bud appeared in the 2nd instar, and with the growth of the instar, the wing bud gradually emerge. Notably, whether there are wing buds or not is an important feature to distinguish psyllid nymph from whitefly nymph. The newly hatched adults are light yellow in colour. After 2-3 days, they turn to a brown or green with pale markings including a white band on the abdomen. After 5 days, the body colour changes to a mixture of grey-black and white (Pletsch 1947; Wallis 1955) Adults live from 20 to 62 d, with females usually outliving males by two to three times depending on the host plant (Pletsch 1947; Yang and Liu 2009; Yang *et al*. 2010). The total development period of *Bactericera cockerelli* depends on many factors, such as host plant, temperature, haplotypes and so on. For example, immature *Bactericera cockerelli* developed faster (24.1 d) when fed on eggplant than on bell pepper (26.2 d) (Yang and Liu 2009). The total lifecycle of *Bactericera cockerelli* on tawa was 27.5 d, followed by poroporo with 30 d, and finally kumara with 9 d (Puketapu 2011). Research showed that the average developmental period of nymph and total lifecycle of North-western haplotype of *Bactericera cockerelli* on the host were longer (25.5 and 31.1 d, respectively) than those of the Western and Central haplotypes (Mustafa *et al*. 2015). Additionally, the developmental time of immature and total stages were negatively correlated with the temperatures between 8 and 27°C (Tran *et al*. 2012)

1.3.2.1.3 Reproductive ability

Potato psyllid adults have multiple mating behaviour. The first mating usually takes place within 2-3 d after emergence. Adults can lay eggs after mating, while the oviposition period may last up to almost 50 d, with an average fecundity of 300-500 eggs per female (Pletsch 1947; Yang and Liu 2009; Yang *et al*. 2010). There are several factors that affect the Vg production, oocyte maturation and oviposition of *Bactericera cockerelli*, including host plants, symbiotic bacteria, hormone and so on. Dr Thinakaran indicated that *Bactericera cockerelli* prefer settling and oviposition on potato and tomato, and chose to settled on pepper, eggplant, and silverleaf nightshade only when potatoes and tomatoes were absent in field, however, *Bactericera cockerelli* adults prefer larger host plants, regardless of the species being tested (Thinakaran *et al*. 2015). Additionally, there is also the oviposition preferences on the same plant cultivars (Liu and Trumble 2006). Previous studies shown that *Candidatus* Liberibacter

solanacearum-infection reduced *Bactericera cockerelli* reproductive output, including Vg1-like expression, oocyte development, and egg production (Frias *et al*. 2018). Virgin females not only could produce mature oocytes, laid several eggs, but also JH III involved in regulating Vg production and oocyte development (Ibanez *et al*. 2017).

1.3.2.1.4 Host adaptability

However, there is a preference of *Bactericera cockerelli* for different host plants. Commonly, Citrus psyllid feeds mainly on the plants in the Solanaceae (potato family), including important crop and common weed species, of which *Solanum tuberosum*, *Lycopersicon esculentum*, *Capsicum* spp. *Solanum melongena*, and *Piper nigrum* etc. are its favorited economic crops (Butler and Trumble 2012; Teulon *et al*. 2009; Puketapu and Roskruge 2011), suggesting that there is still a difference on the adaptation of *Bactericera cockerelli* on Solanaceae plants. Potatoes and tomatoes are the most favorited host plants for *Bactericera cockerelli*, and outdoor plants are vulnerable to psyllid attacks. During the preoviposition period, egg incubation, nymphal development, and total developmental time were longer for psyllids reared on nightshade (*S. dulcamara*) than potato, respectively (Mustafa *et al*. 2015). In New Zealand, psyllid can lay eggs on a common weed Solanum nigrum, but its nymphs fail to survive. Additionally, the psyllid nymphs also cannot complete development on anther weed (Solanum *pseudocapsicum*). Although Solanaceae plants are the typical developmental hosts, a few species of Convolvulaceae, including bindweed and sweet potato are also recognized as the breeding hosts of *Bactericera cockerelli* through rearing trials (Martin 2008; Puketapu and Roskruge 2011) and field investigates (Horton *et al*. 2017; Wallis 1955). *Bactericera cockerelli* quickly died on the Convolvulaceae species that harboured Periglandula and contained ergot alkaloids, suggesting that the survival and development of *Bactericera cockerelli* on Convolvulaceae might be closely related to the fungal symbionts on the plants (Kaur *et al*. 2018).

1.3.2.1.5 Temperature adaptability

Weather is an important factor influencing the biology and damage potential of *Bactericera cockerelli*, which is more suitable for warm but not hot temperatures (Wallis 1955). The optimum temperature for *Bactericera cockerelli* development was approximately 27°C, while oviposition, hatching and survival rates decreased significantly at 32°C and stopped at 35°C (Yang and Liu 2009; Yang *et al*. 2010; Butler and Trumble 2012). The number of generations varies considerably among regions, usually ranging from three to seven depending on the

temperature. Both nymphs and adults have stronger cold-resistant capacity, with nymphs surviving at -15°C and 50% of adults surviving at -10°C for more than 24 h. High temperature and wind are the primary factors that drive the migration of *Bactericera cockerelli* in late spring in n North America, furthermore, colder weather is more conducive to population outbreaks *Bactericera cockerelli* during migration (Munyaneza 2010; Butler and Trumble 2012).

1.3.2.2 Tomato potato psyllid outbreak and damages

1.3.2.2.1 Psyllid yellows

Both adults and nymphs feed upon the phloem using piercing-sucking mouthparts, of which secretion forms white crystal "psyllid sugar" or honey dew. In general, nymphs can cause psyllid yellows (PY) disease in the host plants due to their inherent toxicity. In 1931 Dr. Richards found that psyllid yellows could not be produced on potato when the nymph infestations were low (less than 15 individuals), but that symptom could appear within 4-6 d as the number of nymphs increased (Richards 1931), moreover, the symptoms of PY will appear when at least 8 nymphs feed on 2-week-old tomato plants (Liu and Trumble 2006). *Bactericera cockerelli* adults still failed to produce PY symptoms on tomato while their densities reached to 1,000 individuals per plant, however, adults were able to produce disease symptoms on tomato seedlings (Daniels 1954).

PY disease is systemic, and the whole plant becomes infected. The symptoms of PY include chlorosis or reddening/purpling of leaves, erectness of new leaves, shortened internodes, enlarged nodes, aerial tubers, reduced growth, premature senescence, and plant death (Pletsch 1947). This indicated that the diagnostic features of PY were yellowing and upturning of the margins in young leaf. PY disease resulted in a significant decrease in the yield of potatoes and tomatoes. Smaller and poorer fruit and was formed from tomato infected by PY, and tubers from potato plants are tiny, misshapen, flabby, and have a rough skin, which are associated with various defects, such as early and weak germination, as well as smaller plants (Cranshaw 1993). There is an unacceptable yield loss due to *Bactericera cockerelli* infestation. In California, it was one of the worst pests in greenhouse tomato production with losses exceeding 80% in 2001 and 50% in 2004 (Liu and Trumble 2007). In western Nebraska alone, a 25% yield loss of potatoes equalled to 27,200 metric tons.

1.3.2.2.2 Zebra chip

Zebra chip (ZC), was first reported in 1994 in potato plantations near Saltillo Mexico, it is a new and economically disastrous potato disease (*Solanum tuberosum,* L.) that has been reported in commercial potato fields in the United States, Central America, New Zealand, and Mexico (Munyaneza 2010; Munyaneza *et al*. 2007; Teulon *et al.* 2009). Although it is not known if there will be any negative effect on human health that eating the products processed from ZC-infected potato tuber, the symptom pattern that a severe dark and light striped in raw and fried chips affects their taste and makes commercial value significantly reduced (Munyaneza 2012).

ZC was found to be linked to a previously undescribed strain of the bacterium liberibacter, tentatively called "*Candidatus* Liberibacter solanacearum" (CLso). This liberibacter is associated with Huanglongbing or citrus greening, the most destructive disease of citrus, which occurs in Asia, Africa, and the Americas. The liberibacter is phloem-restricted, Gram-negative, non-culturable bacteria belonging to the genus *Alphaproteobacteria* of which transmitting vector is the *Bactericera cockerelli* (Buchman *et al.* 2011; Butler and Trumble 2012). Lso is an important disease that severely damage to the yield and quality of its host crops such as potatoes and tomatoes (Soliman *et al*. 2010), of which losses reached up to millions of dollars in the United States, Mexico, Central America and New Zealand. The symptoms of this pathogen infection in plants include leaves crimp, yellowing, secondary rooting proliferation, stunted development, and sharply reduced or even total crop failure. The profiles of plant volatile were altered by Lso infection, and infected plants initially recruited herbivores but later repelled them. However, there was a lower fecundity that infected psyllids compared to uninfected psyllids (Nachappa *et al*. 2011).

There are many biological and abiotic factor influenced on CLso feeding and transmission, Liberibacter development, and ZC symptoms expression. For example, the proportion of successful acquisition and inoculation of CLso increased with the feeding area and the vector number, however, there was no effect on the disease progress by bacterial quantity injected or psyllid numbers (Munyaneza 2012). Transmission efficiency of CLso does not differ between males and females, but varies relative to the psyllid developmental stage that that adults are highly efficient than nymphs on transmitting this bacterium (Buchman *et al*. 2011), as well as associated with CLso colonization in insect salivary glands and CLso copy numbers >10,000 per psyllid (Sengoda *et al*. 2018). Additionally, CLso haplotypes were also involved in their

infections in plant species, including two haplotypes (A and B) related to diseases in potatoes and other solanaceous plants, whereas haplotype (C) in carrots infected by the psyllid *Trioza apicalis* (Munyaneza 2012). CLso seems to be sensitive to heat, with temperatures lower than 16°C or higher than 35°C slowing the growth of the Liberibacter. There was a similar temperature preference between those two species that the 27°C was preferred by *Bactericera cockerelli* reproduction and liberibacter development in the plant (Munyaneza 2010; Munyaneza *et al*. 2012), as well as the highest CLso titters in the adult potato psyllid occurred at approximately 28°C (Henneet *et al*. 2010).

1.4. Perspective on the development of IAS management platform and the need of an enhanced compensation system

1.4.1 Interdisciplinary framework for platform development of IAS management

Successful biosecurity policy will require shared responsibility between government, academia, industry and community stakeholders, with technological innovations in surveillance, monitoring, data sharing and analytics playing an important role in addressing the risks presented by invasive and pathogenic exotics to natural ecosystems. Most importantly, any future initiatives must strike a balance between the use of policy, scientific data, education, public engagement and economic incentives to ensure the adoption of holistic approaches to biosecurity, with greater investment in strategies to control threats that compromise biodiversity, in addition to industry and human health. Fragmented approaches, undertaken in isolation without cross-disciplinary support are no longer adequate to ensure the biosecurity in the future (Lott and Rose 2016).

Increasingly plant protection authorities seek to develop integrated decision making through economists and scientists working within an interdisciplinary framework. The collection of papers combines contributions from leading academics and influential policy makers and provides cohesive international perspectives on the use of science and economics, as well as their integration, to progress the development of integrated multi-disciplinary plant health policy making around the world (MacLeod 2015). Risk analysis of species invasions linked to biology and economics, is increasingly mandated by international and national policies, and enables improved management of invasive species.

1.4.2 Enhanced Compensation System is needed in IAS-specific policy

With world globalization and economic trade increasing, the threat from IAS colonizing outside their native habitat has increased drastically (Levine and D'Antonio 2003). The payment from Owner Reimbursement Costs (ORC) decreases the potential obstacle from the property owners, and provide an incentive for stakeholders to report suspected emergency plant pests (EPPs). However, there are still a lot of room to expand the framework of ORC, which is only designed to cover the payment caused by the incursion management of the emergency plant pests (EPPs), while the introduced pests might have created damages to the stakeholders and there are also risks of failure in the eradication of the pest and cause much more damage and continued losses. Since the public (especially the stakeholders) are essential and important in the management of IAS, the development of similar compensation policies for the (potential) invasive species at different stages of the invasion process, which also can invent the public especially the stakeholders to be more positive in the IAS prevention and control actions, is worthy and necessary for a higher effective and more cost-benefit system of IAS management.

1.4.3 Prevention and management method against fall armyworm

1.4.3.1 Monitoring and scouting

For migratory invasive insects, monitoring and scouting are extremely important for timely responses to the dynamics of pest occurrence and development as well as crop health, in order to formulate comprehensive measures for better prevention and control. These actions must be taken while using the minimum cost to keep the FAW population below the economic threshold level.

In China, entomological radar and vertical-pointing searchlight-traps have been used to monitor the population dynamics of migratory insects, such as *H. armigera* (Feng *et al.* ,2009), *Cnaphalocrocis medinalis* (Fu *et al.* 2014), *Mythimna separata* (Zhao *et al.* 2009), *Loxostege sticticalis* (Feng *et al.* 2004), and *Spodoptera exigua* (Feng *et al.* 2003). The monitoring result of vertical-pointing searchlight-traps showed that the FAW population was first trapped in June and the observation peaks appeared from August to October in eight provinces of China in 2019 (Jiang *et al.* 2020). The blacklight and commercial male trap are recommended for farmers to monitor the field population dynamics of FAW. It is recommended that the height of pheromone traps hung should be 1.5 m above ground and the interval between two traps should be 50 m (Malo *et al.* 2013).

Farmers can scout the different plant growth stages and crop damage to determine the optimum stages for spraying insecticides according to the action thresholds, which are expressed as percentages of plants with typical FAW damage/injury symptoms (Prasanna *et al.* 2018). For the early whorl stage, from vegetative emergence (VE) to 6-Leaf (V6) stages, the action threshold is 10%-30% of the seedlings infested as well as the tassel & silk stage, while it is 30%-50% for the late whorl stage (Prasanna *et al.* 2018). For the method of scouting, farmers can move through the field, and randomly select five locations, or use a "W" scouting pattern or a "Ladder" pattern, while avoiding edges in case of edge effects; 20 plants should be examined for each location (Prasanna *et al.* 2018).

1.4.3.2 Agricultural control

For smallholders, a series of low-cost agricultural control measures is an optimum option to implement as part of an effective IPM strategy against FAW, which will avoid expending huge financial resources. Agricultural approaches use the complex interactions between organisms and their environment to develop techniques to minimize the damage of pests on crops. In this review, we introduce a few agricultural measures against FAW.

During pre-planting, using some traditional measures could reduce the numbers of the FAW population in advance, such as deep ploughing the fields to expose pupae to sunlight and predatory birds, which can effectively reduce the base number of the population (Prasanna *et al.* 2018). Planting transgenic/Bt insect-resistant maize varieties is also a very effective measure to reduce the damage by FAW and could be an alternative method to pesticides. Bt maize is commonly used to control FAW, which will influence the bioindicators of FAW including oviposition preference (Tellez-Rodriguez *et al.* 2014), larval dispersal (Malaquias *et al.* 2017), control efficacy (Horikoshi *et al.* 2016; Botha *et al.* 2019) and fitness costs (Jakka *et al.* 2014). The use of transgenic maize expressing bacterial Bt proteins (e.g. Cry1F) has been commercially employed to control this pest since 2003 (Siebert *et al.* 2008). However, in 2010, resistance of the FAW population to transgenic maize with Cry1F toxin was first detected in Puerto Rico (Storer *et al.* 2010). This resistance was attributed to an amino acid mutation in an ATP binding cassette subfamily C2 (SfABCC2) gene, which causes a decrease in binding to Cry1F toxin (Banerjee *et al.* 2017). Developing new insecticidal targets is an urgent need due to the emergence of Bt-resistant FAW populations.

For smallholders, some mechanical/physical methods are also recommended as management options to reduce the economic loss caused by FAW, such as handpicking and crushing the egg masses and larvae, or using ash, sand, sawdust or dirt into whorls to desiccate young larvae (Food and Agriculture Organization of the United Nations 2018). The "push and pull" strategy is a very useful agroecological method to control agricultural pests. Planting minor attractant plants or repellent plants in crop fields could reduce pest damage to major crops. Field experiments showed that maize intercropped with other plants helps to reduce the abundance of FAW. Compared with monocultured maize, intercropping with leguminous crops of bean (*Phaseolus vulgaris*), soybean (*Glycine max*) and groundnut (*Vigna unguiculata*) significantly reduce FAW attack by up to 40% (Hailu *et al.* 2018) (https://www.insectslimited.com/history-of-pheromones). Some other plants, i.e. row intercropping with marigold (*Tagetes erecta*) and border intercropping with Napier grass (*Pennisetum purpureum*) seemed effective for sustainable management of FAW (http://www.icipe.org/news/icipe-push-pull-technology-halts-fall-armyworm-rampage).

1.4.3.3 Divergence of sex pheromone and sex attractant application

Sex pheromones are applied worldwide for pest control as they present several advantages compared to traditional pesticides, such as nontoxicity, high specificity, and the possibility to apply very small amounts. The first major pheromone component of FAW, (Z)-9-tetradecenyl acetate (Z9-14: OAc), was identified in 1967 (Sekul and Sparks 1967). Subsequently, other minor components were identified by analyzing the female pheromone glands and volatiles, including dodecyl acetate (12: OAc), (Z)-7-dodecenyl acetate (Z7-12: OAc), 11-dodecenyl acetate (11-12: OAc), and (Z)-11-hexadecenyl acetate (Z11-16: OAc) (Tumlinson *et al.* 1986). The effectiveness of trapping in the field was first investigated in 1976 (Mitchell and Doolittle 1976). Since then, sex pheromones have been used to suppress and monitor FAW populations worldwide for more than 40 years and research has focused on investigating their differences and applications.

The practical effect of sex pheromones varies with geographical ranges and strains: the pheromone lures from North America and Europe were not effective against FAW in Brazil (Batista-Pereira *et al.* 2006), Costa Rica (Andrade *et al.* 2000) or Mexico (Malo *et al.* 2001). Some evidence points to geographic differences of the female sex pheromone blend in FAW (Batista-Pereira *et al.* 2006; Unbehend *et al.* 2014; Cruz-Esteban *et al.* 2018). For example, while females from Brazil (Batista-Pereira *et al.* 2006) produce (E)-7-dodecenyl acetate (E7-

12: OAc), those from Florida, Louisiana or French Guyana do not (Tumlinson *et al.* 1986; Groot *et al.* 2008; Lima and McNeil 2009). For the Florida populations, the ratios of sex pheromone components from female glands was 4.9 (12: OAc): 3.1 (Z7-12: OAc): 1.7 (11-12: OAc): 3.5 (Z11-16: OAc): 86.9 (Z9-14: OAc). For the Brazilian populations, the sex pheromone consisted of Z7-12: OAc, E7-12: Ac, 12:OAc, (Z)-9-dodecenyl acetate (Z9-12:OAc), Z9-14:OAc, (Z)-10-tetradecenyl acetate (Z10-14:OAc), tetradecyl acetate (14:OAc)/(Z)-11-tetradecenyl acetate (Z11-14:OAc), Z11-16:OAc, and their relative proportions were 0.8 : 1.2 : 0.6 : traces : 82.8 : 0.3 : 1.5 : 12.9, respectively (Batista-Pereira *et al.* 2006). In addition, by adding E7-12: Ac to the major component Z9-14: OAc and critical secondary component Z7-12: OAc, the effectiveness of trapping for Brazilian populations was significantly improved (Batista-Pereira *et al.* 2006).

Two groups have independently studied the strain-specific differences of the component concentration of sex pheromone in female FAW under laboratory and field environments. Both studies have shown that there are strain-specific differences in relative amounts of the different pheromone components (Groot *et al.* 2008; Lima and McNeil 2009; Unbehend *et al.* 2013). One group found a significantly higher relative amount of Z11-16: OAc, and lower relative amounts of Z7-12: OAc and Z9-12: OAc in the corn-strain females compared to rice-strain females in the Florida population (Groot *et al.* 2008). Another group found the opposite result with a significantly larger relative amount of Z9-14: OAc as well as lower relative amounts of Z7-12: OAc and Z11-16: OAc in corn-strain females compared to rice-strain females in the Louisiana population (Lima and McNeil 2009). These diametrically opposed results suggest that both geographic variation and strains contribute to the differentiation of sex pheromone composition of FAW females.

In China, the effects of four different commercial sex attractants on trapping FAW showed that the protection of BLB (Shenzhen Bailebao Bio-Agricultural Technology Co. Ltd) was optimum to monitor the occurrence dynamic of FAW. The average number attracted by BLB lure was 137 individuals per trap, and the trapping performance of BLB lure was stable within 30 days. However, the numbers significantly decreased during the following 30 d, particularly after 50 days (Che *et al.* 2020).

1.4.3.4 Chemical control

Chemical insecticides are heavily used to control FAW (Yu *et al*. 2007). Before the 1980s, insecticides, from organophosphates (methyl parathion, etc.), carbamates (carbaryl, etc.) to pyrethroids (cypermethrin, etc.), were the main method to control FAW in most countries in the Americas (Pitre 1986). Until recently, more than 57 active chemical ingredients with nine modes of action were used against FAW (Table 1-3, not all represent insecticides). Among them, 47 active ingredients were used in the Americas in FAW native regions, while 34 and 20 active ingredients were respectively used in FAW invaded regions in Africa and Asia (Prasanna *et al.* 2018; Gutierrez-Moreno *et al.* 2019) (http://www.moa.gov.cn/govpublic/ZZYGLS/202002/t20200221_6337551.htm).

In the native regions in the Americas, FAW developed resistance to more than 29 insecticides with six modes of action (Gutierrez-Moreno *et al.* 2019). Some insecticides are not suggested for use in the invaded regions of Africa and Asia, such as Methomyl (Pitre 1988), Thiodicarb (Gutierrez-Moreno *et al.* 2019), Tralomethrin and Fluvalinate (Leibee and Capinera, 1995) (Table 1-3), due to the high resistance of FAW. To delay the development of insecticide resistance, eight compound preparations (Emamectin Benzoate × Indoxacarb, Emamectin Benzoate × Hexaflumuron, Emamectin Benzoate × Lambda-cyhalothrin, Emamectin Benzoate × Chlorfenapyr, Emamectin Benzoate × Lufenuron, Emamectin Benzoate × Tebufenozide, Lambda-cyhalothrin × Chlorantraniliprole, and Lambda-cyhalothrin × Diflubenzuron) were recommended by the Ministry of Agriculture and Rural Affairs of China for emergency prevention and control of FAW as there are no legally registered insecticides for FAW.

Although 57 chemicals are listed in Table 1-3 that could be used against FAW, some of them are highly hazardous pesticides (HHPs) that are acknowledged to present particularly high levels of acute or chronic hazards to health or environment according to internationally accepted classification systems such as the World Health Organization (WHO) and the Globally Harmonized System of Classification and Labelling of Chemicals (GHS). If these HHPs are used, adequate precautions must be taken during application.

Table 1-3. Chemical insecticides used against *Spodoptera frugiperda*.

Active ingredient	Used in continents	Active ingredient	Used in countries
Acetylcholinesterase (AChE) inhibitors		**Nicotine acetylcholine receptor (nAChR) allosteric modulators**	
Chlorpyrifos	America, Africa	Spinetoram	America, Asia
Methomyl	America	Spinosad	America, Africa
Thiodicarb	America	Acetamiprid	America, Africa, Asia
Acephate	America, Africa, Asia	Cartap	Asia
Carbaryl	America, Africa	Thiamethoxam	America, Africa, Asia
Carbosulfan	Africa	Thiacloprid	America
Trichlorfon	America	Imidacloprid	Africa
Profenofos	Africa	**Inhibitor of chitin biosynthesis**	
Phenthoate	America	Triflumuron	America, Africa
Methyl-parathion	Africa	Chlorfluazuron	America, Africa
Methamidophos	America	Teflubenzuron	America
Malathion	America, Africa	Novaluron	America
Fenitrothion	America, Africa, Asia	Lufenuron	America, Africa, Asia
Diazinon	America, Africa	Diflubenzuron	America, Asia
Dimethoate	America, Africa	Hexaflumuron	Asia
Sodium channel modulators		**Ryanodine receptor (RyR) allosteric modulator**	
Permethrin	America, Africa	Flubendiamide	America, Africa
Zeta-cypermethrin	Africa	Chlorantraniliprole	America, Africa, Asia
Deltamethrin	America, Africa, Asia	Cyantraniliprole	America, Africa, Asia
Alpha-cypermethrin	America, Africa	Tetrachlorantraniliprole	Asia
Beta-cyfluthrin	America, Africa	**Ecdysone agonists / moulting disruptors**	
Beta-cypermethrin	America	Chromafenozide	America
Bifenthrin	America, Africa	Tebufenozide	America, Asia
Cyfluthrin	Asia	Methoxyfenozide	America
Cypermethrin	America, Africa	**Glutamate-gated chloride channel (GLUCL) allosteric modulators**	
Fenpropathrin	America, Asia	Emamectin benzoate	America, Africa, Asia
Gamma-cyhalothrin	America	Abamectin	Africa
Lambda-cyhalothrin	America, Africa, Asia	**Uncouplers of oxidative phosphorylation via disruption of proton gradient**	
Tralomethrin	America	Chlorfenapyr	America, Africa, Asia
Pyrethrum	America, Africa	**Voltage-dependent sodium channel blockers**	

Fluvalinate	America	Indoxacarb	America, Africa, Asia
Etofenprox	America		
Esfenvalerate	America, Africa		

1.4.3.5 Biological control

Biological control enables reduced contamination of the producer, product, and consumer and offers an economically and environmentally safer alternative to synthetic insecticides that are being used. Natural enemies include parasites, predators and entomopathogens. A great diversity of natural enemies of FAW has been reported in the Americas, Africa, and Asia (Molina-Ochoa *et al.* 2003; Prasanna *et al.* 2018; Shylesha *et al.* 2018). As the native regions of FAW, the Americas have the most abundant parasitoids (~150 taxa) against FAW, which have been recorded from 13 families, nine in Hymenoptera, and four in Diptera (Molina-Ochoa *et al.* 2003). Among them, the egg parasitoids (*Trichogramma pretiosum*, *Trichogramma atopovirilia* and *Telenomus remus*) (Beserra *et al.* 2005; Pomari *et al.* 2013), larval parasitoids (*Campoletis sonorensis* and *Chelonus insularis*) (Jourdie *et al.* 2009), and pupae parasitoids (*Diapetimorpha introit* and *Ichneumon promissorius*) (Molina-Ochoa *et al.* 2003) were widely used to control FAW. In Africa, eight parasitoids of FAW from three families were recovered in west, central and east Africa, including *Chelonus curvimaculatus*, *Chelonus cf maudae*, *Coccygidium luteum*, *Cotesia icipe*, *Cotesia* sp. *Charops ater*, *Charops* sp. and *Telenomus* sp. Studies in southern India recorded five species of larval parasitoids: *Coccygidium melleum*, *Campoletis chlorideae*, *Eriborus* sp. *Exorista sorbillans*, and *Odontepyris* sp. (Sharanabasappa *et al.* 2019). In China, *Telenomus remus* (Zhao *et al.* 2020), *Trichogramma pretiosum* (Zhu *et al.* 2020), *Trichogramma dendrolimi* (Tian *et al.* 2020), and *Trichogramma chilonis* (Li *et al.* 2019b) are the dominant parasitoids of FAW.

The presence of insect predators for both eggs and larvae are important to keep FAW populations under control. The earwigs *Doru lineare* and *Doru luteipes* prey on FAW eggs and larvae (Pasini *et al.* 2007; Sueldo *et al.* 2010). The predators *Picromerus lewisi* and *Arma chinensis* mainly prey on 6th instar larvae of FAW (Tang *et al.* 2019a, b). Two species of predacious bugs, *Eocanthecona furcellata* (Wolff) and *Andrallus spinidens* (Fabr.) (Hemiptera: Pentatomidae) were found to effectively prey on FAW (Shylesha and Sravika 2018).

Several reviews have summarized the entomopathogen resources or potential biopesticide options of FAW and their application status (Bateman *et al.* 2018; Chen *et al.* 2019). Bt is a common biopesticide used to control pests including FAW. The soil bacterium *B. thuringiensis* produces multiple crystal (Cry) proteins or vegetative insecticidal proteins (Vip3A) that are toxic to FAW (Singh *et al.* 2010). In addition, the fungi *Beauveria bassiana*, *B. brongniartii*, *Metarhizium anisopliae*, *Metarhizium rileyi*, *Nomuraea rileyi* and *Paecilomyces fumosoroseus*

have been studied as potential entomopathogens for the control of FAW (Altre and Vandenberg 2001; Carneiro *et al.* 2008; Grijalba *et al.* 2018). The nematodes *Heterorhabditis* and *Steinernema* also effectively control FAW (Garcia *et al.* 2008).

1.4.3.6 Viruses associated with *Spodoptera frugiperda*

SfMNPV is a member of the Group II *Alphabaculovirus* of the Baculoviridae family, which can cause FAW larval mortality rates of more than 90% (Castillejos *et al.* 2002; Simon *et al.* 2012). Numbers of different isolates of SfMNPV have been isolated in North, Central and South America (Berretta *et al.* 1998; Simon *et al.* 2012; Barrera *et al.* 2015). SfMNPV was first studied as a potential bioinsecticide for management of FAW in 1999. Spraying with 1.5×10^{12} viral occlusion bodies (OBs)/ ha caused approximately 40% mortality of FAW larvae at two day post application (Williams *et al.* 1999).

As a biological insecticide, the efficacy of SfMNPV and its speed of killing insects are affected by many factors, such as virulence of different isolates, larval instars, the amount of feeding viral OBs, formulation applied, and environmental conditions. Some studies indicated that diverse isolates had different efficacies: 3AP2 is a fast-killing isolate compared to the wild-type isolate Sf3, and the LT_{50} of the 3AP2 isolate was at least 30 h less than Sf3 when applied in the greenhouse and in the field (Behle and Popham 2012). There is a higher mortality of FAW and longer persistence on crop foliage caused by granular formulation than the aqueous spray application (Castillejos *et al.* 2002). To improve the efficacy of SfMNPV, a variety of SfMNPV formulations were produced for biological control of FAW. Recombinant baculoviruses containing two proteases with insecticidal activity decreased the time to kill insects, thus showing great potential for application in IPM programs (Gramkow *et al.* 2010). Nearly w90% of FAW was controlled by combining SfMNPV with 3 ppm Spinosad, which was 12.5-32% greater than the treatment with SfMNPV alone in a maize field (Mendez *et al.* 2002). Some studies indicated that microencapsulated SfMNPV also has the potential for improving FAW management (Gomez *et al.* 2013). A Colombian SfMNPV was microencapsulated by spray drying with a pH dependent polymer. Viral insecticide activity was not affected by microencapsulation, and the process provided effective protection from UVB radiation (Kurmen *et al.* 2015). Wettable powder formulations utilizing microencapsulation of SfMNPV OBs provide useful advantages related to half-life and photostability of viruses and retain the same efficacy under field conditions. In addition, adding 1% boric acid increased mortality induced by the virus compared to application of granules

containing virus alone in a field trial (Cisneros *et al.* 2002). Importantly, it was reported that a leading biopesticide company, Certis, USA, has obtained the license to develop and manufacture a commercial biopesticide product for field application in selected countries around the world based on Corpoica's SfMNPV strain NPV003 and formulation technology (https://www.certisusa.com/news/releases/news_12112017_certis_usa_licenses_new_virus_technology_for_control_of_fall_armyworm).

Spodoptera frugiperda granulovirus (SfGV) is a member of *Betabaculovirus* of the Baculoviridae family. A granulovirus of FAW in Columbia, South America, was first reported by Steinhaus (1957). SfGV attacks only the fat body, causes a proliferation of cells, and requires a relatively long time to produce mortality. One SfGV isolate was evaluated in a co-infection process and was demonstrated to enhance the insecticidal activity of *Lymantria dispar* NPV (Lepidoptera: Lymantriidae), reducing its mean lethal concentration (LC_{50}) by 13-fold (Shapiro, 2000). Other studies obtained a similar synergic effect in co-infection of GV and NPV, due to the enhancins of baculovirus isolates (Hoover *et al.* 2010; Mukawa and Goto 2011). SfGV has been poorly studied compared to SfMNPV, with relatively few SfGV isolates being characterized.

1.4.3.7 Botanicals for FAW management

Some plant derived pesticides, referred to as botanicals, have good performance in insecticidal activity. They have diverse biological activities resulting in high mortality, extended larval duration, decreased pupa weight, insecticidal effects, growth inhibition, antifeedant effects, reduced fecundity, and sublethal and acute toxicity. Rioba *et al.* (2020) have reviewed the opportunities and scope for botanical extracts and products for the management of FAW in Africa (Rioba and Stevenson 2020). They summarized the efficacy and potential of 69 plant species from 31 families including *Azadirachta indica*, *Schinnus molle*, and *Phytolacca dodecandra*. In China, Lin *et al.* (2020) estimated the indoor toxicity and control effect of azadirachtin in a maize field for FAW. Azadirachtin has good toxicity and antifeedant activity on FAW, and the control effect reached a peak at seven days after treatment (Lin *et al.* 2020).

1.4.4 Prevention and management method against tomato potato psyllid

1.4.4.1 Monitoring and sampling

Currently, early detection and management of *Bactericera cockerelli* is key to reducing the reproduction of this insects, and the spread of ZC in the field. Sticky card traps are commonly used as the monitoring tools in the greenhouse and the field, for example, yellow sticky is suitable for monitoring *Bactericera cockerelli* activity in specific areas but is not very effective to estimate the population density in the field (Butler and Trumble 2012; Martini et al. 2012). However, the neon-green sticky might be better than yellow sticky in monitoring adult potato psyllid (Henne et al. 2010). In addition, sexual pheromone attraction is also an important method for monitoring *Bactericera cockerelli* population (Guédot et al. 2011).

Sweep nets or vacuum devices were usually applied for adult sampling in the field, but egg and nymph samplings need to be visual examined on leaves, which may require to use a field hand lens (Butler and Trumble 2012). The proposed new method called "the leaf washing method or LWM" was to quickly extract and count *Bactericera cockerelli* nymphs from leaves in potatoes fields (Martini et al. 2012). Previous studies indicated that there was an "edge effect" that more psyllids appeared in border areas than within the field (Martini *et al*. 2012), and a similar effect is found with ZC infected potato plants on edges. The juvenile *Bactericera cockerelli* in tomato fields exhibited an edge effect and aggregated distribution, and individuals were mainly located on the bottom of leaves, however, *Bactericera cockerelli* were mostly distributed on the top and middle of the potato plant and the bottom of the leaves (Prager *et al*. 2014; Butler and Trumble 2012). Based on the study, they established the binomial sequential sampling plan for *Bactericera cockerelli* in potato and tomato fields, respectively.

1.4.4.2 Culture control

Crop planting time is closely related to the level of *Bactericera cockerelli* infestation and ZC damage, but there are significant geographical differences. In some areas of the Lower Rio Grande Valley of southern Texas, potato crops grown early are more susceptible to psyllid and ZC damage than those grown in the middle or late stages (Munyaneza 2010), however, this trend was not found in potato fields located north of the Lower Rio Grande Valley. The reasons for this difference have yet been unclear, but it may due to different Lso infection rate in overwintering and migrating *Bactericera cockerelli*. Additionally, coloured mulches, as a promising method of growing control, can be used for managing *Bactericera cockerelli* populations on tomato plants in home garden in Colorado, for example, the population density

of *Bactericera cockerelli* on tomato plants was significantly reduced by aluminum and white plastic mulches in Colorado's home garden (Demirel and Cranshaw 2006).

1.4.4.3 Chemical control

Chemical pesticides remain the primary method of controlling potato psyllid (Gharalari *et al*. 2009; Butler *et al*. 2011), but even with heavy insecticides use, psyllids are difficult to control. It is important because psyllids are primarily found on the underside of leaves, which are difficultly contacted by insecticides (Butler and Trumble 2012). Additionally, the intensive use of pesticides causes psyllid to develop severe resistance (Morales *et al*. 2018), such as neonicotinoid insecticides (Szczepaniec *et al*. 2019). Specific pesticides are required for the different life stages of *Bactericera cockerelli*, and even insecticides that have been shown to control adults are not necessarily effective against nymphs or eggs (Gharalari *et al.* 2009). Cyanoacrylamide and spinetoram showed a high rate and the highest activity against adults, respectively, whereas cyantraniliprole and oxamyl (low and high rates, respectively) were effective against nymphs (Echegaray *et al.* 2017). Moreover, the season-long regimes were more effective than insecticide applications in controlling the pest (Echegaray *et al.* 2017). Caution must therefore be exercised in the selection and application of insecticides, requiring growers to consider the stage of *Bactericera cockerelli* and then choose the time of application accordingly. In recent years, common insecticides used to control *Bactericera cockerelli* includes pyrethroids, neonicotinoids, acephate, metamidophos, thiacloprid, buprofezin, abamectin, cyanoacrylamide, cypermethrin, deltamethrin, lambda-cyhalothrin, esfenvalerate, spinosad, spirotetramat, imidacloprid, thiamethoxam, spiromesifen, dinotefuran, pyriproxyfen, pymetrozine, and flupyradifurone (Butler and Trumble 2012; Guenthner *et al.* 2012).

1.4.4.4 Biological control

The rapid development of resistance leads to the gradual reduction of control efficiency of chemical pesticides. Presently, biological control has become one of the most promising methods for controlling *Bactericera cockerelli* population (Butler and Trumble 2012; Prager and Trumble 2018). There were many species recorded as the natural enemies of *Bactericera cockerelli*, including the predators chrysopid, nabids, coccinellids, mirids, geocorids, anthocorids, mites (Munyaneza 2012; Pineda *et al.* 2020), the parasitoids *Tamarixia triozae* and *Metaphycus psyllidis* (Liu *et al.* 2019), and several entomopathogenic fungi, such as *Beauveria bassiana*, *Metarhizium anisopliae*, *Zoophthora radicans, Isaria fumosorosae* and so on (Villegas-Rodriguez *et al.* 2017; Liu *et al.* 2019). However, the control effect is often not

determined by a single species, and a complex interaction network is usually formed among different natural enemies. In recent years, a comprehensive control strategy combining various biological control agents has been used to control pest populations (Ullah and Lim 2017). Through combining the predators *Dicyphus hesperus* with parasitic wasps *Tamarixia triozae* could improve the control for *Bactericera cockerelli* in tomato (Calvo *et al.* 2018). The combination of *Amblydromalus limonicus* with *B. bassiana* suspensions or *Typha orientalis* pollen can significantly reduce the population number of *Bactericera cockerelli* and increase the crop yield (Liu *et al.* 2019). In addition, the efficiency of biocontrol is also affected by biological and abiotic factors, such as host plant and pesticides. the host plant and experience can regulate the searching behaviour of the parasitoid *Tamarixia triozae* (Hernández-Moreno *et al.* 2019). *A. limonicus* could suppress *Bactericera cockerelli* populations on pepper but not tomato cultivars, speculating that it is related to leaf morphology and generation time of *Bactericera cockerelli* on different plant species (Kean *et al.* 2018). A certain mortality of *Tamarixia triozae* was caused by the insecticides, including soybean oil, imidacloprid, and abamectin on Solanaceous crops (Morales *et al.* 2018).

Chapter Two

Statement of Contribution

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- ➢ The sum of all co-author contributions is equal to 100% less the candidate's stated Contribution

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Modelling seasonal habitat suitability for wide-ranging migratory species: Invasive fall armyworm *Spodoptera frugiperda* in Australia

Abstract

Seasonal migration of migratory species could result in a changing of their potential distribution and habitat suitability during different season. We know very little about the potential seasonal distribution of many wide-ranging migratory species. Fall armyworm, *Spodoptera frugiperda*, native to the Americas, is a widespread and harmful invader in Africa, Asia and Oceania and attracting increased attention worldwide. In order to better understand the seasonal geographic distributions of *Spodoptera frugiperda*, we employed ecological niche models of MaxEnt to predict potential year-round breeding and seasonal distribution for *Spodoptera frugiperda* on a global scale and in Australia. A total of 74 MaxEnt models were built using various combinations of regularization multiplier, feature class and climatic variables, and the best model based on model evaluation metrics was selected, with an evaluation of dominant climatic factors that control its distribution. Our results suggest that the temperature factor was the most important variable affecting the seasonal distribution of *Spodoptera frugiperda*. No matter in the world or in Australia, year-round breeding distribution model predicted smaller portions of fall armyworm's ranges than the seasonal model. Fall armyworm had a high remaining invasion potential in Australia, posing a significant threat to its biosecurity, food security and agricultural productivity.

2.1 Introduction

Biological invasion is one of the most daunting and grand challenge environmental problems facing the World in the 21st century (Blakeslee *et al.* 2011). Invasive alien species seriously threaten the economy, natural resources, global biodiversity, and human health (Early *et al.* 2016; Pimentel *et al.* 2005). Due to the global climate change, habitat destruction, the increase in global trade and transportation in the past few years, the spread risk and invasion rate of invasive alien species have increased significantly (Meyerson and Mooney 2007; Westphal *et al.* 2008). Controlling and eradicating invasive alien species would be costly and impossible once they are established in a new region (Wan and Yang 2016a). Predicting the potential geographical distribution of invasive alien species before their introductions or early invasions

would be of great benefit to their preventions (Waage and Reaser 2001; Liebhold *et al.* 2015). Hence, identifying the potential habitat extents where invasive alien species are likely to establish is critical for the early warning, prevention and control of their invasions to mitigate ecological and economic damages (Jiménez-Valverde *et al.* 2011).

During the last decades, ecological niche models (ENMs) are increasingly being applied to predict the potential distribution, habitat suitability, and possible dispersal routes of species (Jiménez-Valverde *et al.* 2011; Zhu *et al.* 2017). Among these modeling tools, Maximum Entropy (MaxEnt) has attracted increasing attention as a widespread tool to predict the potential distribution of invasive alien species with various advantages, such as using continuous and categorical data, incorporating interactions between different variables (Phillips *et al.* 2006), and avoiding commission errors (Pearson and Cohoon 1999). It has a better performance in predicting species distribution, compared to other ecological niche models, (Elith *et al.* 2006; Phillips and Dudík 2008; Phillips *et al.* 2017).

It is well known that migratory species can show strong plastic responses to climatic changes, as they can move fast from one area to another in search of resources and suitable conditions (Ponti *et al.* 2018). Seasonal migration of migratory species could result in a changing of their potential distribution and habitat suitability during different times of the year (Engler *et al.* 2014; Hayes *et al.* 2015). Therefore, the shifts in migratory species distribution ranges depended on species specific flight abilities affecting the extent of suitable areas available for their survival (Araújo and Pearson 2005), this may require new methods to uncover and new paradigms to understand.

Seasonal distribution and migratory patterns are relatively well known for many noctuid moth species (Hu *et al.* 2015). An advantageous noctuid moth model for studying seasonal migratory processes is *Spodoptera frugiperda* (J.E. Smith), commonly known as the fall armyworm, rated as one of the world's top ten plant pests by the International Center for Agriculture and Biological Sciences (CABI). Fall armyworm is native to the tropical and subtropical regions of the Americas and has long been a major agricultural problem in the Western Hemisphere (Luginbill 1928; Johnson 1987). Fall armyworm invaded Nigeria and Ghana in January 2016 (Goergen *et al.* 2016; Cock *et al.* 2017) and spread through virtually all of Sub-Saharan Africa within two years (Nagoshi *et al.* 2018). The United Nations Food and Agriculture Organization is particularly concerned about the threat to global food security and issued a global warning

about the fall armyworm in August 2018 (FAO, 2018). With the rapid expansion of international trade and transportation, and its long-distance migration capability, it spread rapidly across Africa, Asia (Guo *et al.* 2018; Ma *et al.* 2019), posing as increasing risk to cash crops in large parts of the world (FAO, 2018; Early *et al.* 2018).

Australia is the world's sixth largest country by land mass, and it contains large areas of rice, maize, and wheat cultivation, which constitutes approximately 8% of the world's agriculture trade. Australia has tropical and subtropical climate characteristics that could permit population of fall armyworm establishment. According to the latest news, fall armyworm has been confirmed in surveillance traps in Torres Strait islands of Saibai and Erub and Bamaga north of Queensland, its first major introgression into Oceania since January 2020 (IPPC, 2020). Then, fall armyworm has established a breeding population and spread rapidly across Northern territory and western Australia. Therefore, Australia is a region of particular concern for the invasion of fall armyworm, which faces a significant threat to its biosecurity, food security and agricultural productivity from the fall armyworm. Here, we employ ecological niche models of MaxEnt to predict its potential seasonal hazard regions during different seasons based on global-scale occurrence records of fall armyworm and its ecological niche requirements. Combinations of regularization multiplier, feature class and climatic variables were evaluated to select the best fitting model. Together, understanding the potential year-round breeding and seasonal distribution during different seasons will be beneficial for the monitoring and early warning of this pest in Australia.

2.2 Materials and methods

2.2.1 Species distribution

The fall armyworm is native to tropical regions of the western hemisphere from the United States to Argentina (Luginbill 1928; Sparks 1979), and is widely distributed in North America, Central America, the Caribbean, South America (Early *et al.* 2018). Since 2016 when the fall armyworm was first invaded into the Eastern Hemisphere (Goergen *et al.* 2016), it spread quickly across 47 countries of Africa (Day *et al.* 2017; Stokstad 2017; Nagoshi *et al.* 2018; Feldmann *et al.* 2019). Fall armyworm has first invaded India in Asia (Sharanabasappa *et al.* 2018), then spread across 18 countries of South, Southeast and East Asia with remarkable speed (Guo *et al.* 2018; Ma *et al.* 2019). Since 2020, fall armyworm has been confirmed in Torres Strait islands of Saibai and Erub and Bamaga north of Queensland, its first major introgression into Oceania. At the present, fall armyworm has infested crops in 112 countries and regions all

over the world (Figure 2-1). Its long-distance migration capability, coupled with increasing transportation and international trade, significantly increases the risk that its global spread will continue.
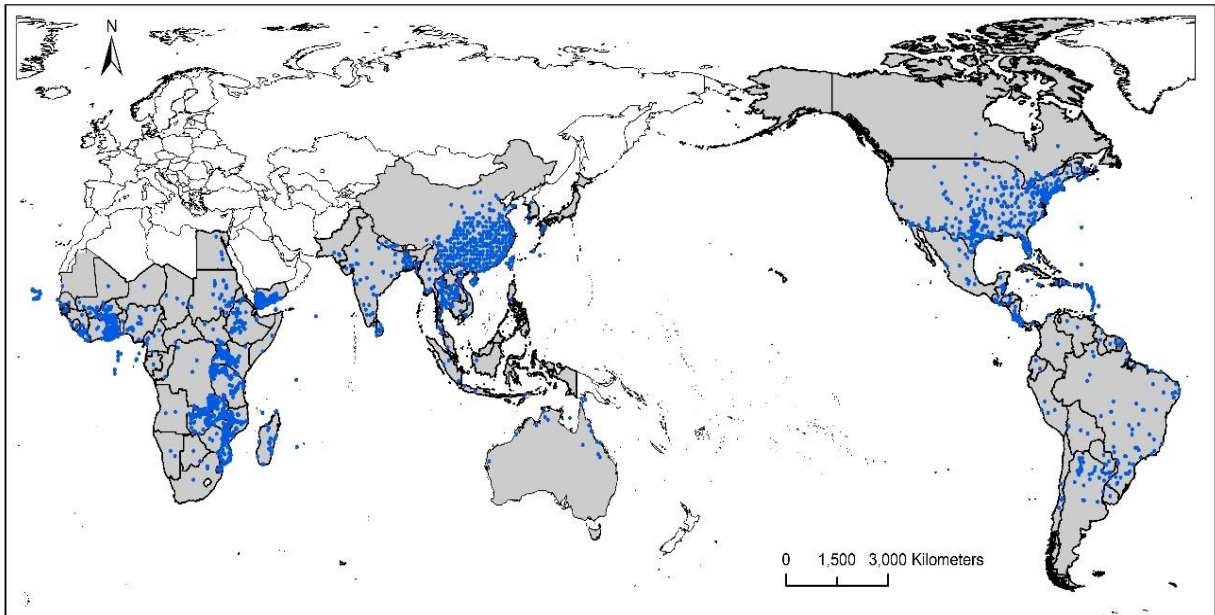
Figure 2-1. Global geographical distribution map of *Spodoptera frugiperda* Grey areas represent occurrence regions, blue point represents occurrence sites for the current modeling.

2.2.2 Occurrence data collection and filtering

Occurrence data for the fall armyworm were obtained from the Global Biodiversity Information Facility (http://www.gbif.org), the Center for Agriculture and Bioscience International, the Invasive Species Compendium (http://www.cabi.org/isc), the European and Mediterranean Plant Protection Organization, the Plant Quarantine Data Retrieval system (http://www.eppo.int), the FAW Monitoring & Early Warning System of FAO (http://www.fao.org/fall-armyworm/en/), and relevant published studies. These occurrence data collected for different sources and regions varied in term of quality and precision, which might impact the robustness of model calibrations and evaluations, and therefore required careful vetting and inspection. In total, we collected more than 10,000 occurrence records for the fall armyworm after deleting the wrong, repeatable and impractical distribution point. Occurrence site records were converted to a .csv file format that included species name, latitude, and longitude, as required for use in MaxEnt.

The elimination of spatial clusters of localities is important for model calibrating and evaluation.

When spatial clusters of localities exist, often models are over-fit towards environmental biases and model performance values are inflated (Veloz 2009; Boria *et al*. 2014). To eliminate spatial autocorrelation and sampling bias, we created a grid of 1 km×1 km cell using ArcGIS and randomly selected a single point from each cell (Jiménez-Valverde *et al.* 2011; Boria *et al.* 2014). After filtering, 5738 locations remained and used for the modeling represented in Figure 2-1.

Moreover, since fall armyworm inhabit different geographic areas during different times of the year due to seasonal migration (Westbrook *et al.* 2016), therefore, we analyzed seasonal ranges separately, distinguishing between year-round breeding and seasonal hazard areas. Their year-round breeding season was considered as the coldest season, which is from December to February in the Northern Hemisphere, from June to August in the Southern Hemisphere. All the months are considered the seasonal hazard season because of the large occurrence range of fall armyworm due to its long-distance migration. The distribution points of fall armyworm in the coldest season were selected from species occurrence data. After filtering, 3390 locations were considered to contain year-round breeding populations, and 5738 locations were considered to contain seasonal populations.

2.2.3 Environmental variables selection

Climatic factors are more important than non-climatic factors for determining the potential distribution of invasive species on a larger geographical scale (Guisan *et al*. 2013). Non-climatic factors such as topography, bionomics and occupancy dynamics, may function on a local scale (Hortal *et al.* 2010). Therefore, climatic factors are considered to be the main factors that determine species niches and have been widely used for invasive species niche modeling (Qiao *et al*. 2013; Zhu and Qiao 2016). Climatic variables used for modeling were obtained from the WorldClim database, version 2.1 (http://www.worldclim.org/). All variables were recorded between 1950 and 2000 with a spatial resolution of 30 arc-seconds, corresponding to approximately 1 km at the equator (Zhu *et al.* 2012).

Multicollinearity among the predictor variables may hamper the analysis of species-environment relationships, therefore, some causal variables must be discarded if others can better statistically explain the variation in the response variable (Elith *et al.* 2010). To establish a high-performance model with fewer variables, cross-correlations (Pearson correlation coefficient, r) for each pairwise comparison of all climatic variables were tested. Only one

variable from each set of the highly cross-correlated variables (r > 0.75) was retained for further study based on both correlation analyses (Zhu *et al*. 2017) (Tables 2-1 and 2-2). We excluded variables that combined temperature and precipitation because they display artificial discontinuities between adjacent grid cells in some areas (Escobar *et al*. 2014). We also retained the variable with the greatest unique contribution, determined from jackknife tests of variable importance in MaxEnt model (Peterson and Cohoon 1999). Five environmental variables were included for the year-round breeding populations of *Spodoptera frugiperda* prediction in the final analysis, including Bio1, Bio6, Bio7, Bio12, and Bio14. Five were retained for the seasonal populations of *Spodoptera frugiperda* modeling, Bio1, Bio3, Bio7 and Bio8, and Bio14.

Table 2-1. Correlation analysis of environmental variables for the year-round populations of *Spodoptera frugiperda*.

Environmental variables	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19
Bio1	1.000																		
Bio2	-0.055	1.000																	
Bio3	-0.203	0.128	1.000																
Bio4	0.136	0.141	-0.886	1.000															
Bio5	0.836	0.380	-0.407	0.454	1.000														
Bio6	0.695	-0.502	0.301	-0.461	0.247	1.000													
Bio7	0.103	0.719	-0.578	0.748	0.602	-0.623	1.000												
Bio8	0.823	-0.092	-0.470	0.477	0.740	0.402	0.265	1.000											
Bio9	0.838	-0.139	0.180	-0.269	0.574	0.860	-0.244	0.474	1.000										
Bio10	0.926	0.013	-0.501	0.481	0.914	0.448	0.368	0.881	0.652	1.000									
Bio11	0.862	-0.114	0.255	-0.376	0.560	0.883	-0.275	0.512	0.928	0.628	1.000								
Bio12	-0.028	-0.310	0.289	-0.376	-0.254	0.250	-0.409	-0.104	0.052	-0.182	0.144	1.000							
Bio13	0.079	-0.230	0.082	-0.214	-0.076	0.182	-0.209	0.005	0.061	-0.030	0.161	0.877	1.000						
Bio14	-0.095	-0.305	0.322	-0.264	-0.308	0.221	-0.430	-0.068	0.010	-0.187	0.040	0.637	0.329	1.000					
Bio15	0.199	0.279	-0.478	0.432	0.420	-0.240	0.538	0.245	-0.045	0.336	-0.030	-0.419	-0.057	-0.609	1.000				
Bio16	0.041	-0.217	0.062	-0.188	-0.096	0.132	-0.183	-0.010	0.011	-0.055	0.111	0.897	0.982	0.342	-0.076	1.000			
Bio17	-0.093	-0.324	0.383	-0.327	-0.330	0.267	-0.485	-0.089	0.045	-0.209	0.071	0.681	0.365	0.982	-0.660	0.371	1.000		
Bio18	-0.185	-0.337	-0.107	0.075	-0.320	-0.099	-0.174	0.056	-0.315	-0.176	-0.240	0.650	0.565	0.509	-0.283	0.609	0.510	1.000	
Bio19	0.113	-0.135	0.483	-0.467	-0.079	0.436	-0.422	-0.151	0.356	-0.060	0.350	0.656	0.494	0.452	-0.394	0.496	0.508	0.110	1.000

Table 2-2. Correlation analysis of environmental variables for the seasonal populations of *Spodoptera frugiperda.*

Environmental variables	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19
Bio1	1.000																		
Bio2	-0.077	1.000																	
Bio3	0.605	0.203	1.000																
Bio4	-0.753	-0.030	-0.922	1.000															
Bio5	0.694	0.191	0.047	-0.128	1.000														
Bio6	0.941	-0.204	0.756	-0.887	0.442	1.000													
Bio7	-0.729	0.315	-0.821	0.930	-0.032	-0.910	1.000												
Bio8	0.727	-0.156	0.198	-0.326	0.660	0.595	-0.359	1.000											
Bio9	0.903	-0.023	0.720	-0.829	0.505	0.922	-0.794	0.447	1.000										
Bio10	0.759	-0.152	0.012	-0.149	0.923	0.548	-0.185	0.759	0.550	1.000									
Bio11	0.956	-0.037	0.786	-0.911	0.493	0.981	-0.867	0.594	0.934	0.543	1.000								
Bio12	0.162	-0.400	0.197	-0.237	-0.120	0.265	-0.350	0.034	0.192	0.006	0.204	1.000							
Bio13	0.350	-0.300	0.262	-0.384	0.039	0.402	-0.430	0.219	0.316	0.133	0.383	0.830	1.000						
Bio14	-0.347	-0.252	-0.242	0.344	-0.257	-0.286	0.201	-0.329	-0.247	-0.170	-0.364	0.463	0.014	1.000					
Bio15	0.453	0.198	0.266	-0.423	0.300	0.382	-0.288	0.387	0.356	0.243	0.463	-0.256	0.226	-0.777	1.000				
Bio16	0.318	-0.293	0.237	-0.366	0.011	0.370	-0.408	0.191	0.288	0.100	0.354	0.853	0.982	0.033	0.204	1.000			
Bio17	-0.300	-0.277	-0.182	0.291	-0.248	-0.228	0.140	-0.297	-0.199	-0.150	-0.311	0.521	0.063	0.986	-0.789	0.076	1.000		
Bio18	-0.084	-0.419	-0.193	0.083	-0.275	-0.047	-0.074	0.091	-0.154	-0.084	-0.100	0.615	0.535	0.314	-0.136	0.578	0.330	1.000	
Bio19	0.123	-0.164	0.303	-0.193	-0.017	0.233	-0.267	-0.094	0.239	0.028	0.172	0.604	0.369	0.422	-0.353	0.367	0.476	0.035	1.000

2.2.4 MaxEnt parameter configuration and best model selection

Previous studies have demonstrated that using the default automatic configuration of MaxEnt may not always be appropriate (Merow *et al*. 2013; Marchioro 2016). It is recommended that the most appropriate model should be selected by evaluating the best potential combination of parameters: regularization multiplier, feature classes (Shcheglovitova and Anderson 2013; Kumar *et al*. 2015). Therefore, we compared models with different feature class and regularization multiplier combinations. MaxEnt includes five basic feature classes: Hinge (H), linear (L), quadratic(Q), product (P), and threshold (T) (Phillips *et al.* 2006; Elith *et al.* 2011). As simple models with great explanatory predictive power can potentially be produced using various combinations of the feature classes (Shcheglovitova and Anderson 2013; Kumar *et al*. 2015), six combinations were tested: L, H, LQ, LQH, LQHP, and LQHPT. The regularization multiplier values were set to 0.5, 1 (default), 3, 5, 7, and 9 based on Wan *et al*. (2020). Combining regularization multipliers and feature classes, we assessed a total of 74 models for two environmental datasets, including two default auto-feature models.

In the MaxEnt model, the area under the curve (AUC) in a receiver operating characteristic (ROC) were employed to evaluate model performance (Ward 2007). AUC is a composite measure of model performance and weights the omission error. AUC values range from 0 to 1, where 1 is a perfect fit and a value of 0.5 or less indicates a prediction no better than random. Useful models produce AUC values of 0.7–0.9, and models with 'good discriminating ability' produce AUC values above 0.9 (Phillips *et al.* 2006; Phillips and Dudík 2008). AUC.diff is the difference between training and testing AUC. Value of AUC.diff is expected to be positively associated with the degree of model overfitting (Warren and Seifert 2011). The following criteria were adopted to select the best model with low complexity and high performance: higher AUC values (>0.8), AUC.diff values approximate to 0.

2.2.5 Seasonal habitat suitability modeling

Once the parameter combination yielding the best model was determined, the MaxEnt model version 3.3.3k (https://www.cs.princeton.edu/~schapire/maxent/) was run with the occurrence data and environmental variables to predict the potential seasonal hazard regions of the fall armyworm during different seasons in Australia. Seventy-five percent of the distribution points were randomly selected for model training, and the remaining 25% were used to test the model (Elith *et al.* 2006; Zhu *et al.* 2012). To increase the accuracy and reliability of modeling results,

the final model was run for 30 replications and output in logistic format (Zhu *et al.* 2017; Wan *et al.* 2020). Potential distribution maps showing unsuitable, suitable habitats for *Spodoptera frugiperda* were then produced using the minimum training presence threshold (MTP). Habitats with logistic output values less than the MTP were regarded as unsuitable, while habitats with values above the MTP were considered suitable.

2.3 Results

2.3.1 Model calibration and evaluation

Overall, 76 MaxEnt candidate models built with various combinations of regularization multiplier, feature class and climatic variables were evaluated to select the best fitting model to predict the potential distribution of fall armyworm. Both AUC and AUC.diff evaluation metrics used to assess model performance varied with different parameter combinations (Figure 2-2). AUC values ranging from 0.85 to 0.90 indicated that all models of fall armyworm's year-round breeding distribution performed better than random (Figure 2-2A). In a similar way, AUC values ranging from 0.72 to 0.82 indicated that all models of fall armyworm's seasonal distribution performed better than random (Figure 2-2B). AUC value changed with different regularization multipliers and feature classes, and its change was generally consistent between the year-round breeding and seasonal distribution models. The models built with the LQHPT feature usually had higher AUC values. All the models usually had lower AUC.diff values, which were regarded as the low degree of model overfitting (Figures 2-2C and 2-2D). Based on the model selection criteria, the best model for the fall armyworm's year-round breeding and seasonal distribution was similar and obtained when using LQHPT feature, a regularization multiplier equal to 1 (Figure 2-2). The performance of the selected best model was better than that of the MaxEnt model obtained using the default settings.
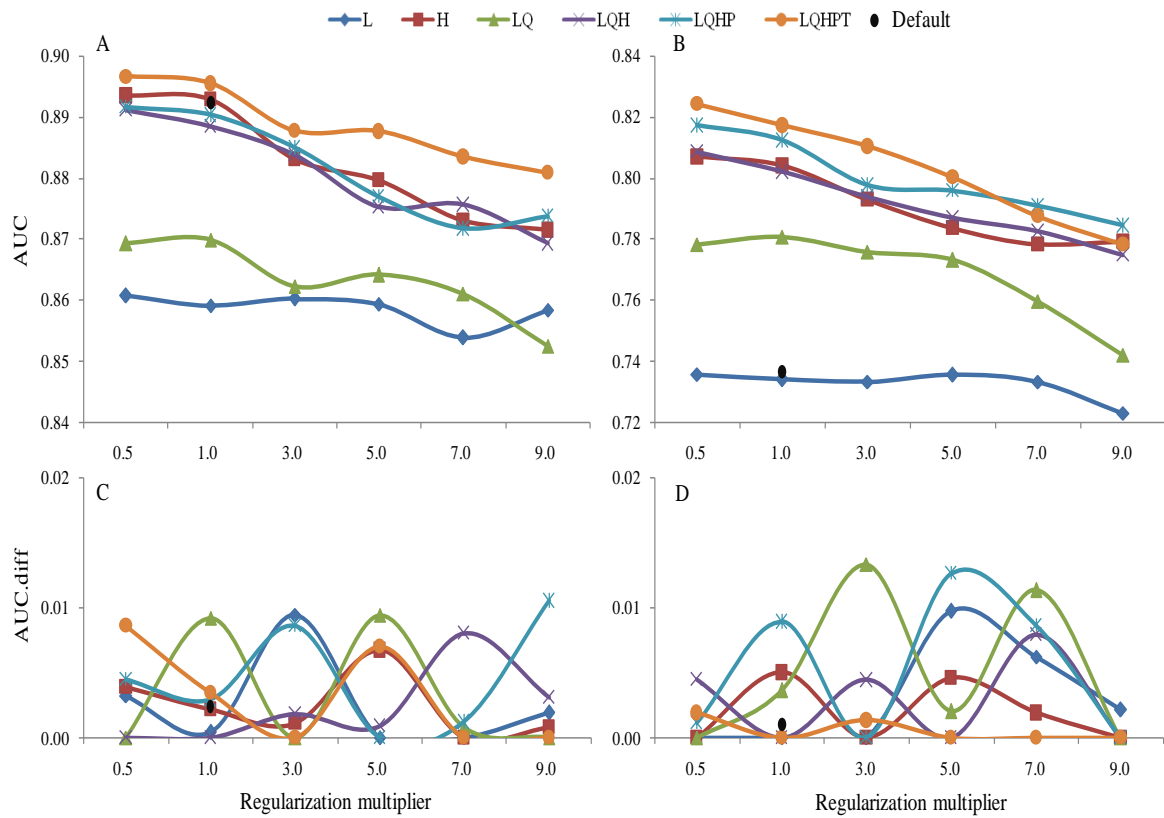
Figure 2-2. Performance statistics for models of *Spodoptera frugiperda*.'s year-round breeding (A, C) and seasonal (B, D) distribution built with various combinations of regularization multiplier, feature class. (Feature abbreviations: L, linear; Q, quadratic; P, product; H, hinge; T, threshold).

2.3.2 Importance of environmental variables

According to the relative contribution of each selected climatic variable in predicting the geographic year-round breeding and seasonal distribution of the fall armyworm. Min temperature of coldest month (Bio6; 70.7%) was the most important variable in explaining the potential year-round breeding distribution of *Spodoptera frugiperda* (Figure 2-3), while Bio7 and Bio1 contributed 14.2% and 10.9% to the prediction respectively. These three variables contributed a total of 95.8% to the performance of the model. Annual mean temperature (Bio1; 59.1%) was the most important environmental variable in explaining the potential seasonal distribution of *Spodoptera frugiperda* (Figure 2-3), while Bio8 and Bio7 contributed 22.2% and 12.4% to model performance respectively. These three factors explained 93.7% of the prediction. The result of the model implied that the temperature factor was the most important variable affecting the year-round breeding and seasonal distribution of *Spodoptera frugiperda*.
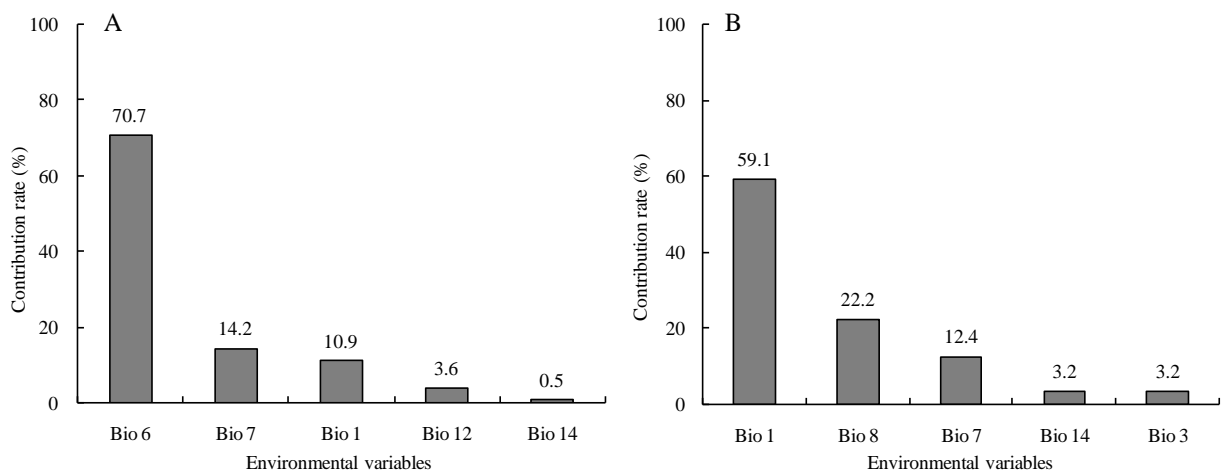
Figure 2-3. The contribution of each selected environmental variable in predicting the habitat suitability of *Spodoptera frugiperda*'s year-round breeding (A) and seasonal (B) distribution models.

2.3.3 Global seasonal habitat suitability of fall armyworm

Predicted global habitat suitability varied considerably between seasonal scenarios. Year-round breeding distribution model predicted smaller portions of fall armyworm's ranges than the seasonal model (Figure 2-4). Overall the model predicted the year-round breeding habitat occupied 16.6% of the global land surface area during the cold season, while the seasonal habitat covered 33.4% of global land surface area. No matter in coldest season or other season, South America, North America, Africa, Asia, and Oceania had a wide range of suitable habitat for *Spodoptera frugiperda*. Of this, year-round breeding suitable habitats were disproportionately found in tropical and subtropical areas in northern and central South America, south of the Sahara Desert of Africa, southern South Asia, Southeast Asia, southern North America and northern Oceania (Figure 2-4A). Potential distribution and suitable habitat of *Spodoptera frugiperda*, however, were highly seasonal due to its strong long-distance migration ability. Fall armyworm widely expand their seasonal damage range into new areas, such as East Asia, central North America, most of Oceania, and parts of Europe (Figure 2-4B). These seasonal predictions for *Spodoptera frugiperda* closely matched its present-day distribution.
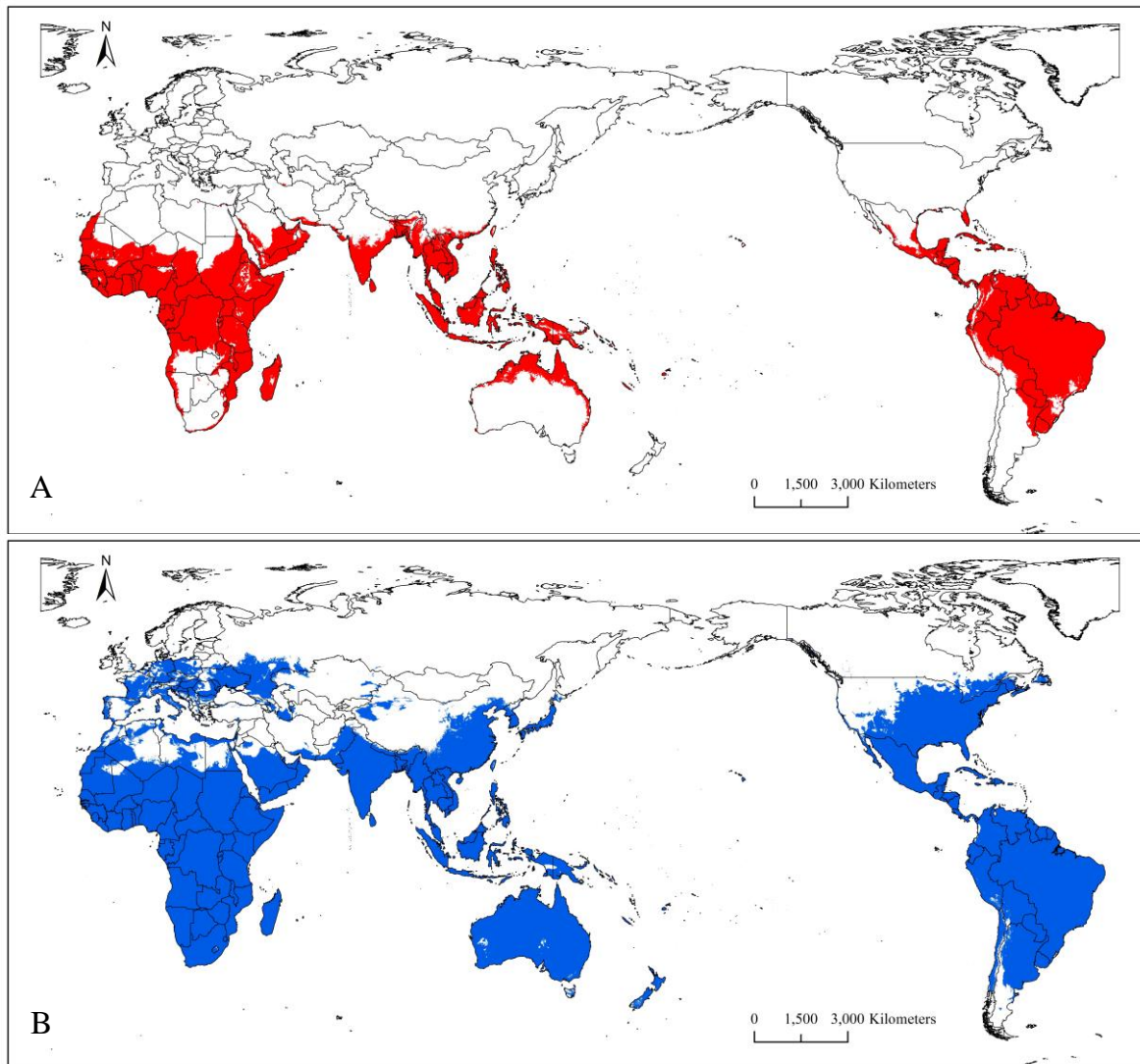
Figure 2-4. Predicted global suitable habitats for the year-round breeding populations and seasonal populations of *Spodoptera frugiperda*. The red area represents year-round breeding distribution during the cold season (A), the blue area represents the potential seasonal hazard region (B).

2.3.4 Seasonal habitat suitability of fall armyworm in Australia

Similar trends were seen for the seasonal habitat suitability of fall armyworm in Australia. The models indicated that fall armyworm had different potential hazard regions for population establishment during the different seasons in Australia. In the cold season, year-round breeding populations of fall armyworm were restricted to parts of northern Australia and coastal areas. The winter breeding area encompassed 20.6% of Australia's total land area, and there were no potential year-round breeding areas in most of central and southern Australia during the cold season. Our model suggested that *Spodoptera frugiperda* could widely extend their seasonal

damage range into central and southern Australia from the winter breeding area. The seasonal suitable habitats of fall armyworm covered almost all (98.5%) land area of Australia, even the central desert and Tasmania, the southernmost island in Australia. Therefore, fall armyworm had constituted a new threat and a potential for further range expansion in Australia during the different seasons.
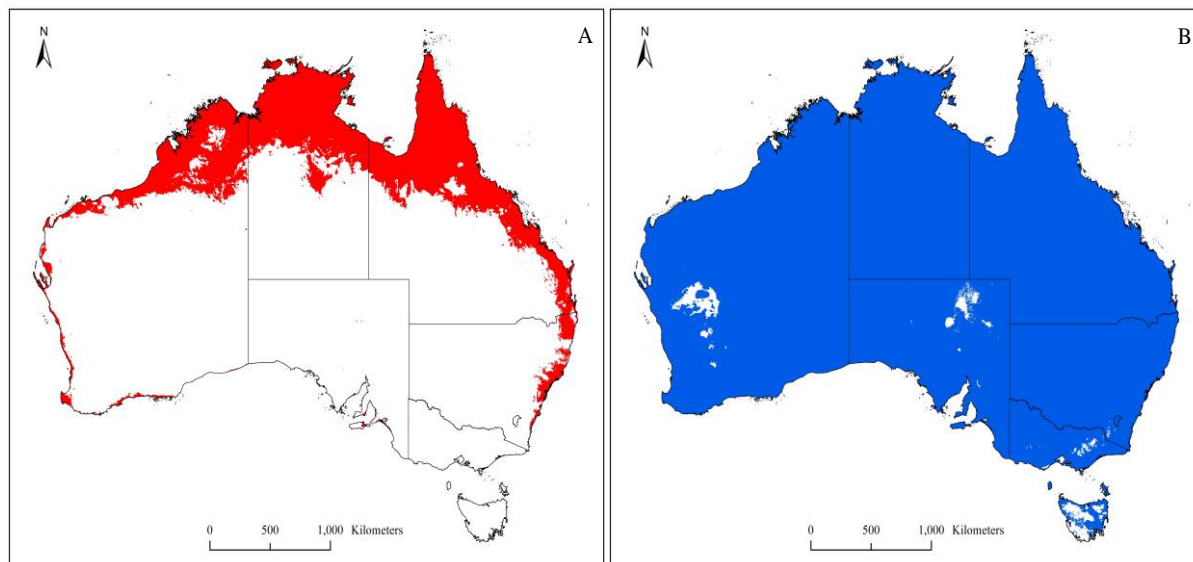
Figure 2-5. Potential suitable habitats for the year-round breeding populations and seasonal populations of *Spodoptera frugiperda* in Australia. The red area represents year-round breeding distribution during the cold season (A), and the blue area represents the potential seasonal hazard region (B).

2.4 Discussion

The fall armyworm can only survive in winter breeding regions in North America that extend up into south Texas and Florida (Sparks 1979; Nagoshi *et al.* 2009). It has a strong long-distance migration ability. During the spring and summer, this pest then re-invades its northern geographic range through successive long-distance flights (Westbrook *et al.* 2016). By the end of the summer, infestations are regularly reported as far north as the provinces of Québec and Ontario in Canada. Seasonal migration of *Spodoptera frugiperda* resulted in a changing of its potential distribution and habitat suitability during different seasons (Westbrook *et al.* 2019). Therefore, the infestation area of the fall armyworm differs among seasons.

Several researches had simulated potential distribution and invasion risk of the fall armyworm in the world (Early *et al.* 2016), Africa (Fan *et al.* 2020), China (Qin *et al.* 2019; Wang *et al.*

2020). Some models indicated that *Spodoptera frugiperda* had a wide range of suitable habitat and a potential for further range expansion to the rest of the world (Early *et al.* 2016). Nevertheless, these predictions for *Spodoptera frugiperda* didn't closely matched its present-day distribution. And little research on the potential seasonal distribution of *Spodoptera frugiperda* during different seasons had been done. In this study, the selected distribution points included the origin and invasion areas of fall armyworm in the Americas, Africa, and Asia, thereby improving the reliability of the predictions. We drew global maps of the year-round breeding and seasonal distribution (Figure 2-4). The prediction results confirmed potential habitat suitability varied considerably between seasonal scenarios. Our model showed that South America, North America, Africa, Asia, and Oceania had a wide range of suitable habitat for *Spodoptera frugiperda* (Figure 2-4). Fall armyworm could widely expand their seasonal damage range into East Asia, central North America, most of Oceania, and parts of Europe from the year-round breeding area (Figure 2-4B). This finding is similar to the potential geographical distribution of fall armyworm suggested by Early *et al.* (2018).

Australia is an island continent with prosperous sea-borne transport that puts it at a high risk for biological invasions through intentional or unintentional pathways (Chen and Xu 2001). Australia has tropical and subtropical climate characteristics to permit the survival and breeding of the fall armyworm, putting food security and agricultural productivity at risk (Early *et al.* 2018). The models indicated that fall armyworm had different potential hazard regions for population establishment during the different seasons in Australia. According to our analysis, *Spodoptera frugiperda* could widely extend their seasonal damage range into central and southern Australia from the winter breeding area, such as parts of northern Australia and coastal areas. Thus, fall armyworm had constituted a new threat and a significant biosecurity risk to Australia.

The accuracy of the model depends on the selection of environmental variables and MaxEnt parameter configuration (Jiménez-Valverde *et al.* 2011; Shcheglovitova and Anderson 2013; Kumar *et al.* 2015). Recent studies suggested the strongest climatic limits on fall armyworm's year-round distribution are the coldest annual temperature and the amount of rain in the wet season (Early *et al.* 2018). In this study, two groups of different environments variables were retained after cross-correlations. It implied that the temperature factor (Bio6 and Bio1) were the most important variable affecting the potential year-round breeding and seasonal distribution of *Spodoptera frugiperda*. Moreover, 76 MaxEnt candidate models built with

various combinations of regularization multiplier, feature class and climatic variables were evaluated to select the best fitting model. We obtained the best model using LQHPT feature, a regularization multiplier equal to 1 (Figure 2-2).

Upon invasion, fall armyworm must overcome a series of challenges such as geographic barriers and differences in climate, hosts, and natural enemies (Richardson and van Wilgen 2004; De Meyer *et al.* 2010). Fall armyworm has a broad host range that includes over 350 plant species (Montezano *et al.* 2018). Australia constitutes approximately 8% of the world's agriculture trade, and these crops (wheat, maize, rice etc.) are all potential food sources for the fall armyworm. Thus, the availability of host plants is probably not a limiting factor for *Spodoptera. frugiperda* invaded Australia. The lack of natural enemies and the suitable climate and temperature are likely to promote its establishment once it has invaded. Agricultural production areas that contain possible habitable locations for the fall armyworm lie along the east coast and the inner regions of Queensland, New South Wales, and Victoria. The island of Tasmania, which mainly produces poppy, pyrethrum, grape, and apples, is also potentially vulnerable, as are areas along coast of western and southern Australia.

More pertinent to the spread of fall armyworm are expanding global travel and trade, which have increased the incidence of alien invasive species all over the world. The impact of human activities on the geographical distribution of fall armyworm cannot be ignored (Early *et al.* 2018). Cock *et al* (2017) speculated that the fall armyworm entered Africa from America as a stowaway on direct commercial flights, and Sharanabasappa's (2018) analysis suggested that the fall armyworm was introduced from Africa to India through imported agricultural commodities. Global travel and trade are the main means by which the fall armyworm moves between continents (Cock *et al.* 2017). Once invasive alien species have established in a new area, it is extremely difficult to eradicate them completely (Liebhold *et al.* 2015). The cost of controlling their spread is extremely high, and predicting their potential geographical distribution is therefore the most effective way to control them (Hobbs and Humphries 1995; Waage and Reaser 2001). Identifying locations where the fall armyworm is likely to establish, and spread is critical for preventing or slowing its invasion and offers an opportunity to mitigate its ecological and economic impacts (Jiménez-Valverde *et al.* 2011; Zhu *et al.* 2017). Given the forecast presented here, regions of Australia with suitable crops and climate urgently require information on how to protect themselves from the fall armyworm.

Chapter Three

Statement of Contribution

Title of Paper	Predicting the potential geographic distribution of *Bactrocera bryoniae* and *Bactrocera neohumeralis* (Diptera: Tephritidae) in China using MaxEnt ecological niche modeling
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Principal Author	**Jing Wan**
Name of Principal Author (Candidate)	Data and literature collection, analysis, structure format, manuscript development
Overall Percentage (100%)	65%
Signature **Date** 04/11/2020	

Co-Author Contributions

By signing the statement of contribution, each author certifies that:

➢ The candidate's stated contribution to the publication is accurate (as detailed above).

➢ Permission is granted for the candidate to include the publication in the thesis

➢ The sum of all co-author contributions is equal to 100% less the candidate's stated Contribution

Name of Co-Author	QI Guo-jun
Contribution to the Paper	Modelling, Manuscript development, revision
Overall Percentage	10%
Signature **Date** 04/11/2020	
Name of Co-Author	MA Jun
Contribution to the Paper	Manuscript development, data analysis, revision
Overall Percentage	6.25%
Signature **Date** 04/11/2020	
Name of Co-Author	Rui Wang
Contribution to the Paper	Modelling, Manuscript development, revision, supervision
Overall Percentage	6.25%
Signature **Date** 04/11/2020	

Name of Co-Author	Yonglin Ren
Contribution to the Paper	Structure format, revision, supervision
Overall Percentage	6.25%
Signature	**Date** 04/11/2020
Name of Co-Author	Simon McKirdy
Contribution to the Paper	Structure format, revision, supervision
Overall Percentage	6.25%
Signature	**Date** 04/11/2020

Predicting the potential geographic distribution of *Bactrocera bryoniae* and *Bactrocera neohumeralis* (Diptera: Tephritidae) in China using MaxEnt ecological niche modelling

Abstract

Bactrocera bryoniae and *Bactrocera neohumeralis* are highly destructive and major biosecurity/quarantine pests of fruit and vegetable in the tropical and subtropical regions in the South Pacific and Australia. Although these pests have not established in China, precautions must be taken due to their highly destructive nature. Thus, we predicted the potential geographic distribution of *Bactrocera bryoniae* and *Bactrocera neohumeralis* across the world and in particular China by ecological niche modeling of the Maximum Entropy (MaxEnt) model with the occurrence records of these two species. *Bactrocera bryoniae* and *Bactrocera. neohumeralis* exhibit similar potential geographic distribution ranges across the world and in China, and each species was predicted to be able to distribute to over 20% of the globe. Globally, the potential geographic distribution ranges for these two fruit fly species included southern Asia, the central and the southeast coast of Africa, southern North America, northern and central South America, and Australia. While within China, most of the southern Yangtze River area was found suitable for these species. Notably, southern China was considered to have the highest risk of *Bactrocera bryoniae* and *Bactrocera neohumeralis* invasions. Our study identifies the regions at high risk for potential establishment of *Bactrocera bryoniae* and *Bactrocera neohumeralis* in the world and in particular China and informs the development of inspection and biosecurity/quarantine measures to prevent and control their invasions.

3.1 Introduction

Invasive species not only pose a threat to global biodiversity but also affect the economy, natural resources, and human health (Pimentel *et al.* 2005; Early *et al.* 2016; Wan and Yang 2016). Due to the increase in global trade and transportation in the past few years, the risk and rate of invasive alien species (IAS) introductions have increased significantly (Meyerson and Mooney 2007; Westphal *et al.* 2008; Lin *et al.* 2011; Aguin-Pombo 2012). Controlling and

eradicating IAS can be challenging and costly once they are established in a new region. Predicting the potential geographical distribution of IAS before their introduction can help develop proactive measures for prevention (Hobbs and Humphries 1995; Waage and Reaser 2001; Liebhold *et al.* 2015). Therefore, identifying locations where IAS are likely to establish is critical for the early detection, prevention, and control of IAS invasions to mitigate ecological and economic damages (Jiménez-Valverde *et al.* 2011; Zhu *et al.* 2017).

Recently, ecological niche modeling (ENM) has emerged as a powerful tool for studying biological invasion and predicting the potential global and regional distribution, habitat suitability, and possible dispersal routes of IAS (Peterson 2001; Barve *et al.* 2011; Jimenez-Valverde *et al.* 2011; Zhu *et al.* 2017). Many modeling approaches, such as the Generalized Linear Model (GLM), Generalized Additive Model (GAM), Bioclimatic Prediction System (BIOCLIM), Climate Change Experiment (CLIMEX), Genetic Algorithm for Rule-Set Production (GARP), and Maximum Entropy (MaxEnt) have been employed in biodiversity, conservation biology and invasion biology studies (Bellard *et al.* 2012; Zhu and Qiao 2016). Among these, MaxEnt is a general- purpose machine learning method with many advantages, such as using continuous and categorical data, incorporating interactions between different variables (Phillips *et al.* 2006), and avoiding commission errors (Pearson *et al.* 2007). It also outcompetes other ecological niche models with a better performance in predicting species distribution (Elith *et al.* 2006; Hernandez *et al.* 2006).

The genus *Bactrocera* contains over 500 fruit fly species and many are considered major pests, leading to quantitative and qualitative losses in crop production in Australia, Oceania and tropical Asia (White and Elson-Harris 1992; Dori *et al.* 1993; Vijaysegaran 1997). For instance, the Queensland fruit fly *Bactrocera tryoni* is one of the most destructive insect pests of fruit and vegetable crops in Australia (Raghu *et al.* 2000; Sutherst *et al.* 2000; Clarke *et al.* 2011), causing an estimated annual lose between 28.5 million and 100 million AUD (Sutherst *et al.* 2000). Among all pest fruit fly species, *B. bryoniae* and *B. neohumeralis* are economically significant due to wide climatic and host range (Raghu and Clarke 2001; Meats 2006; Morrow *et al.* 2015; Royer 2015), with *B. tryoni* causing more damage to fruit and vegetable production (Meats 2006; Royer and Hancock 2012). *Bactrocera bryoniae* and *B. neohumeralis* are widely distributed throughout the tropical and sub-tropical regions of Australia and South Pacific regions (Drew *et al.* 1982; Gillespie 2003), where they either directly damage fruit and vegetable crops or cause phytosanitary restrictions of the entire infected planting area (Dominiak and Worsley 2016).

Bactrocera bryoniae and *B. neohumeralis* are biosecurity/ quarantine fruit fly pests that can be spread from the tropical and subtropical regions of Australia (Dominiak and Worsley 2016). They were first reported and intercepted in China in early 1998, and arrived with pepper *via* a passenger from Australia (Liang *et al.* 1998). Although *B. bryoniae* and *B. neohumeralis* have not yet colonized naturally in China, they are of major concern owing to their destructive nature and frequent interceptions at Chinese ports (Liang *et al.* 2008; Wu 2014). As agricultural trade between Australia and China continue to increase, Australia has become the fourth largest trading partner of China for agricultural products (Yin and Xiao 2007). As a result, there is a growing risk of *B. bryoniae* and *B. neohumeralis* invasions. Therefore, inspection and quarantine are required when importing fruits from Australia.

The invasion of *B. bryoniae* and *B. neohumeralis* will threaten the agriculture production and devastate the fruit industry in China (Liang *et al.* 2008; Li *et al.* 2009). Understanding the habitat suitability for *B. bryoniae* and *B. neohumeralis* establishment across various geographical regions in China is crucial to prevent and control their spread (Li *et al.* 2009). Thus, we aim to predict the potential geographical distributions of these two specie based on habitat suitability. We employ MaxEnt for the prediction using global-scale occurrence records of *B. bryoniae* and *B. neohumeralis* according to the ecological niche requirements. Regions that are environmentally suitable for these two fruit fly species will be identified. The findings of this study will guide the development of the control measures for preventing *B. bryoniae* and *B. neohumeralis* invasions.

3.2 Materials and methods

3.2.1 Species occurrence data

The occurrence data of B. bryoniae and B. neohumeralis were derived from the Global Biodiversity Information Facility (http://www.gbif.org), Center for Agriculture and Bioscience International, Invasive Species Compendium (http://www. cabi.org/isc), European and Mediterranean Plant Protection Organization, Plant Quarantine Data Retrieval system (http://www.eppo.int) and published studies. These datasets provide the most complete and detailed historical and distributional information of B. bryoniae and B. neohumeralis to date.

Niche model predictions tend to overfit around known occurrences, and the performance values of the model are often inflated when using spatial cluster occurrences (Jiménez-Valverde *et al.*

2011; Boria *et al.* 2014). To eliminate spatial autocorrelation and sampling bias, we created a grid of 10 km×10 km cells using ArcGIS and randomly selected one or more single point(s) from each cell. As shown in Figure 3-1, 23 locations of *B. bryoniae* and 33 locations of *B. neohumeralis* were retained after the filtering.
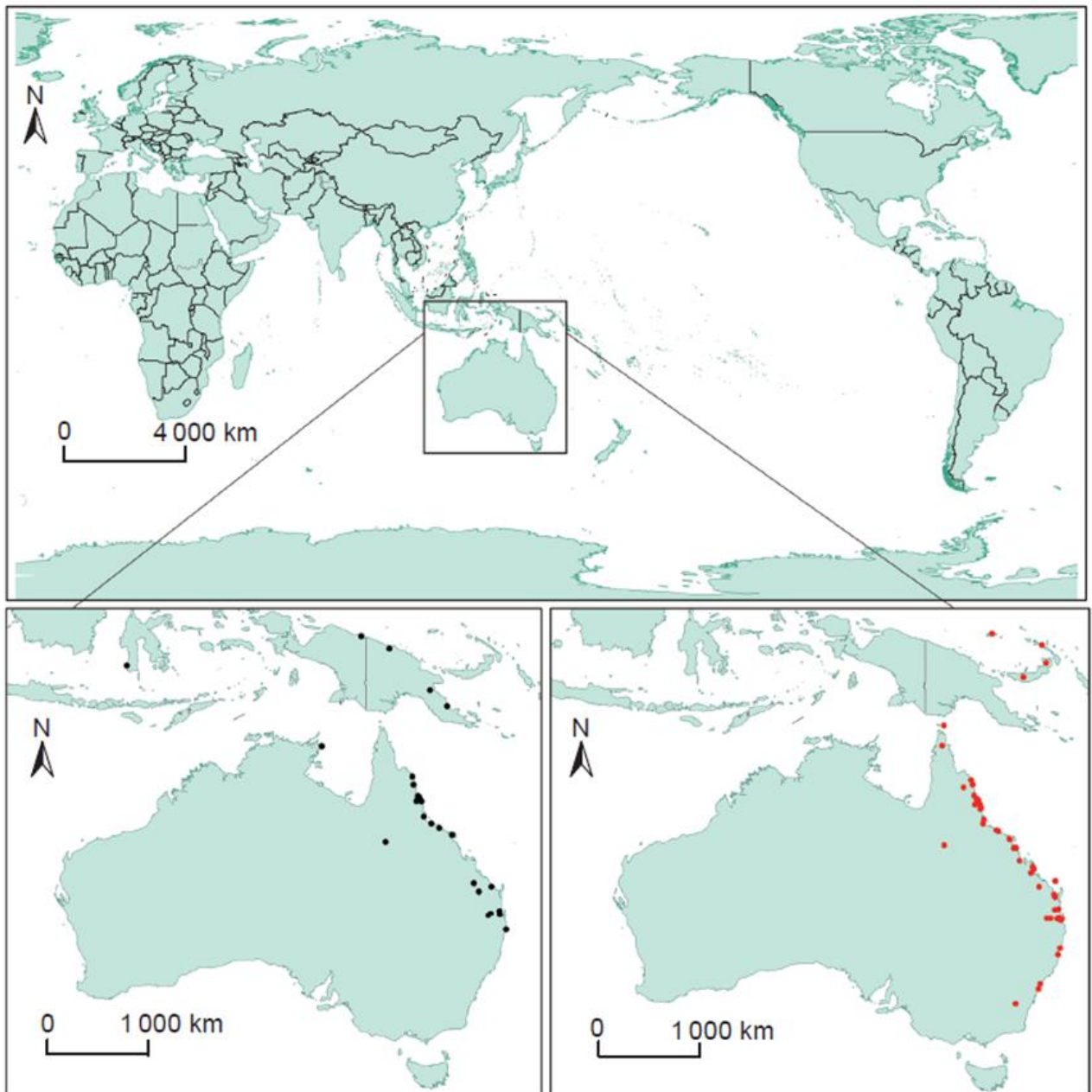
Map inspection number: GS(2020)1908

Figure 3-1. Global occurrence data of *Bactrocera bryoniae* (Black spot) and *Bactrocera neohumeralis* (Red spot) based on the Maxent distribution modelling.

3.2.2 Climatic data

Climatic factors are more important than topographical factors for determining the potential distribution of invasive species on a larger geographical scale (Guisan *et al.* 2013). Non-climatic factors such as bionomics and occupancy dynamics, may function on a local scale (Hortal *et al.* 2010). Therefore, climatic factors are widely used to predict the potential distribution ranges of invasive species on the regional and global scales. Climatic variables used for modeling were obtained from the WorldClim Database (http://www.worldclim. org/). Nineteen climate variables recorded between 1950 and 2000 were used including annual mean temperature (Bio1), monthly mean temperature range (Bio2), isothermality (Bio3), temperature seasonality (Bio4), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6), annual temperature range (Bio7), mean temperature of the wettest quarter (Bio8), mean temperature of the driest quarter (Bio9), mean temperature of the warmest quarter (Bio10), mean temperature of the coldest quarter (Bio11), annual precipitation (Bio12), precipitation of the wettest month (Bio13), precipitation of the driest month (Bio14), precipitation seasonality (Bio15), precipitation of the wettest quarter (Bio16), precipitation of the driest quarter (Bio17), precipitation of the warmest quarter (Bio18), and precipitation of the coldest quarter (Bio19). All climatic variables had a spatial resolution of 2.5 arcminutes (~ 5 km at the equator) (Zhu *et al.* 2012).

3.2.3 Variable selection and statistical analysis

Multicollinearity among the predictor variables may hamper the analysis of the relationship between species distribution and environment. Therefore, some causal variables must be discarded if others can better statistically explain the variation in the response variable (Heikkinen *et al.* 2006). To establish a high-performance model with fewer variables, cross-correlations (Pearson correlation coefficient, *r*) among the climatic variables were tested.

We also assessed the correlations among *B. bryoniae* and *B. neohumeralis* occurrence points and each climatic variable using ArcGIS 10.4. Only one variable from each set of the highly cross-correlated variables (*r*>0.8) was retained for further study based on both correlation analyses (Zhu *et al.* 2012, 2017). Seven variables were included for the *B. bryoniae* prediction, including Bio1, Bio2, Bio4, Bio12, Bio14, Bio15 and Bio18, and six were retained for the *B. neohumeralis* modeling, Bio1, Bio2, Bio7, Bio12, Bio14 and Bio15.

3.2.4 Ecological Niche Modeling

We used MaxEnt (version 3.3.3k, available from https://www.cs.princeton.edu/˜schapire/ maxent/) to predict the potential distribution of *B. bryoniae* and *B. neohumeralis* globally and in China. The parameters of MaxEnt were set as follows: the available feature was auto feature including linear, quadratic, product, threshold and hinge (Phillips *et al.* 2006; Elith *et al.* 2011). The logistic output was used in MaxEnt, which generated a continuous map with an estimated probability of presence between 0 and 1 (Elith *et al.* 2006; Zhu *et al.* 2017).

The selected climatic variables that represent the main factors are considered important determinants of the distribution of *B. bryoniae* and *B. neohumeralis* in China and the world. The MaxEnt analysis randomly selected 75% data for model training, and the remaining 25% data were used to test the model (Zhu *et al.* 2012; Qi *et al.* 2015). In the MaxEnt model, the significance of the variables contributing to *B. bryoniae* and *B. neohumeralis* distribution is represented by the average values of the area under the curve (AUC) of ten model iterations (Elith *et al.* 2010). This suitability analysis provides sensitivity and specificity scores, the average contribution rate of each variable to the model, and the jackknife analysis of the contribution of each variable to the model (Phillips *et al.* 2006; Suwannatrai *et al.* 2017). The habitat suitability for *B. bryoniae* and *B. neohumeralis* was reclassified into four different levels based on the predicted suitable probability: unsuitable (<0.05), low habitat suitability (0.05–0.1), moderate habitat suitability (0.1–0.2), and high habitat suitability (>0.2).

3.2.5 Model evaluation

The AUC of the receiver operating characteristic (ROC) generated by MaxEnt was used to estimate model performance (Wang *et al.* 2007; Ward 2007). AUC values range from 0 to 1, AUC<0.5 suggests random prediction, an AUC value between 0.5 and 0.7 indicates poor performance, an AUC value between 0.7 and 0.9 indicates moderate performance, and AUC>0.9 indicates high performance (Swets 1988; Phillips *et al.* 2006).
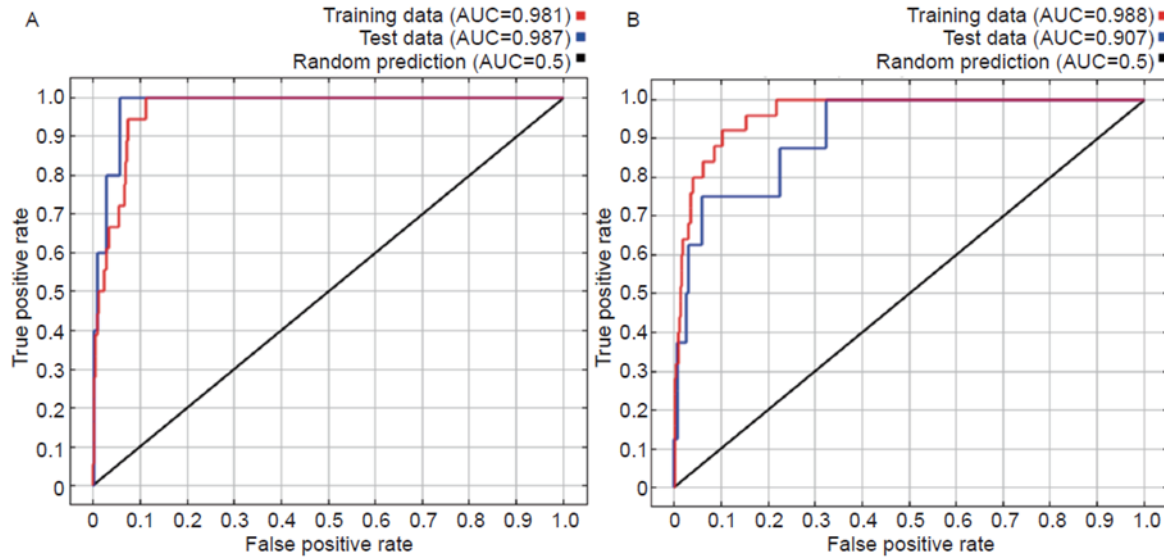
Figure 3-2. Receiver operating characteristic (ROC) curve verification of the prediction for *Bactrocera bryoniae* (A) and *Bactrocera neohumeralis* (B) by MaxEnt. AUC, area under the curve.

3.3 Results

3.3.1 Model performance for potential distribution and environmental variables

Our models showed high predictive accuracy with AUC values above 0.9, indicating that they perform better than random models in predicting the habitat suitability for the two fly species. Specifically, we detect a mean training AUC value of 0.98 and 0.99 (Figure 3-2A), and a test AUC value of 0.99 and 0.91 (Figure 3-2B) for *Bactrocera bryoniae* and *Bactrocera neohumeralis*, respectively.

According to the relative contribution of each selected climatic variable in predicting the geographic distribution of the two fly species (Figures 3-3A and 3-3B), precipitation of the warmest quarter (Bio18; 68.3%) was the most important variable in explaining the potential distribution of *Bactrocera bryoniae* (Figure 3-3A), while Bio4, Bio1, and Bio14 contributed 27.1% to the prediction, these variables contributed a total of 95.4% to the performance of the model. Annual precipitation (Bio12; 46.2%) was the most important environmental variable in explaining the potential distribution of *Bactrocera neohumeralis* (Figure 3-3B), while Bio1, Bio14, and Bio7 contributed 48.7% to model performance, these four factors explained 94.9% of the prediction.
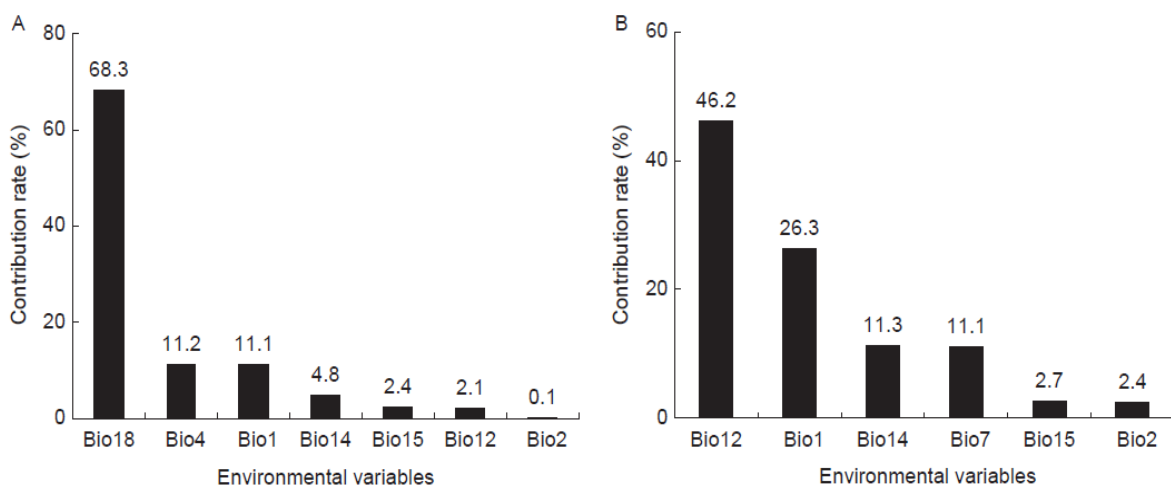
Figure 3-3. The contribution of each environmental variable in predicting the habitat suitability of *Bactrocera bryoniae* (A) and *Bactrocera neohumeralis* (B) in the models. Bio18, precipitation of the warmest quarter; Bio4, temperature seasonality; Bio1, annual mean temperature; Bio14, precipitation of the driest month, Bio15, precipitation seasonality; Bio12, annual precipitation; Bio2, monthly mean temperature range; Bio7, annual temperature range.

3.3.2 The global distribution of *Bactrocera bryoniae* and *Bactrocera neohumeralis*

The global projection results showed that Asia, Africa, South America, North America, and Oceania had a wide range of habitable regions for *Bactrocera bryoniae* (Figure 3-4), occupying 23.04% of the global land surface area—among which 12.29%, 5.24% and 5.51% had high, moderate and low suitability, respectively. The highly suitable habitats for *Bactrocera bryoniae* were mainly distributed in southern Asia, the equatorial region and the southeast coastal areas of Africa, southern North America, northern and central South America, and eastern coastal areas of Australia. The Mediterranean coastal areas, northern and western Australia, southern Africa, central North America, and parts of South America exhibited moderate to low suitability for *Bactrocera bryoniae*.

Compared to *Bactrocera bryoniae*, *Bactrocera neohumeralis* had a relatively wider distribution range (Figure 3-5). The total suitable area of *Bactrocera neohumeralis* accounted for 25.66% of the global land surface area, of which 15.27%, 5.80% and 4.59% were high, moderate and low suitability areas, respectively. Despite an overall wider distribution range, the highly

suitable habitats for *Bactrocera neohumeralis* were like those of *Bactrocera bryoniae*, we detected no significant difference in the moderate and low suitable habitats between *Bactrocera bryoniae* and *Bactrocera neohumeralis*.
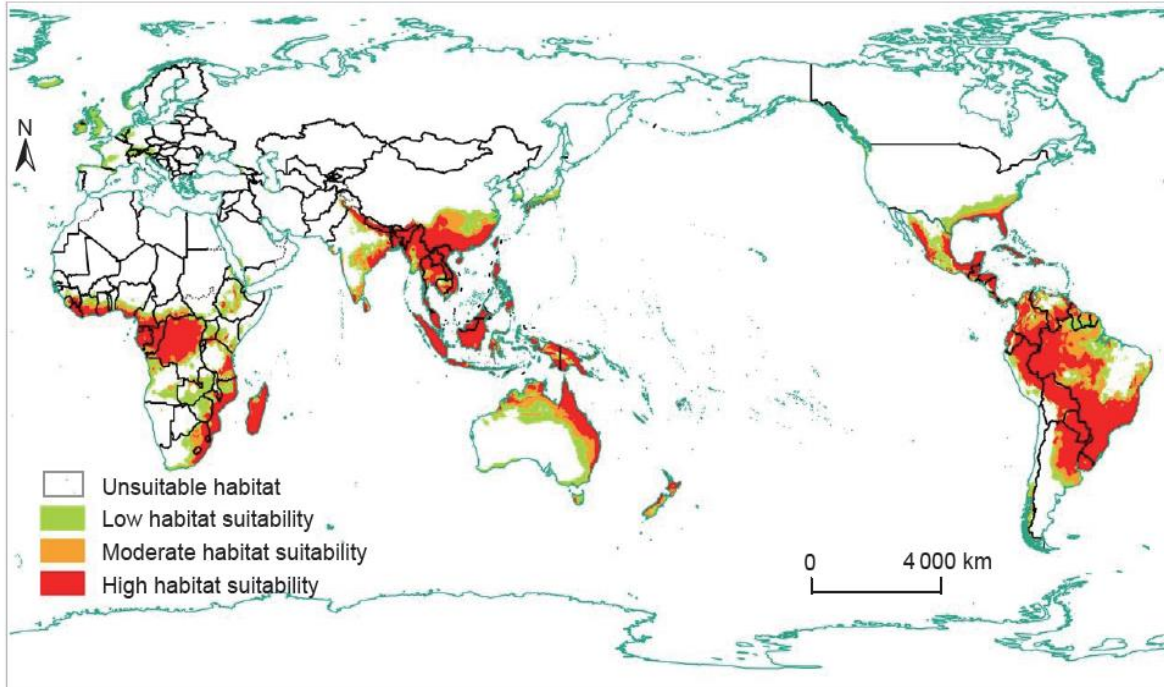
Map inspection number: GS(2020)1908

Figure 3-4. Global habitat suitability map for *Bactrocera bryoniae*.
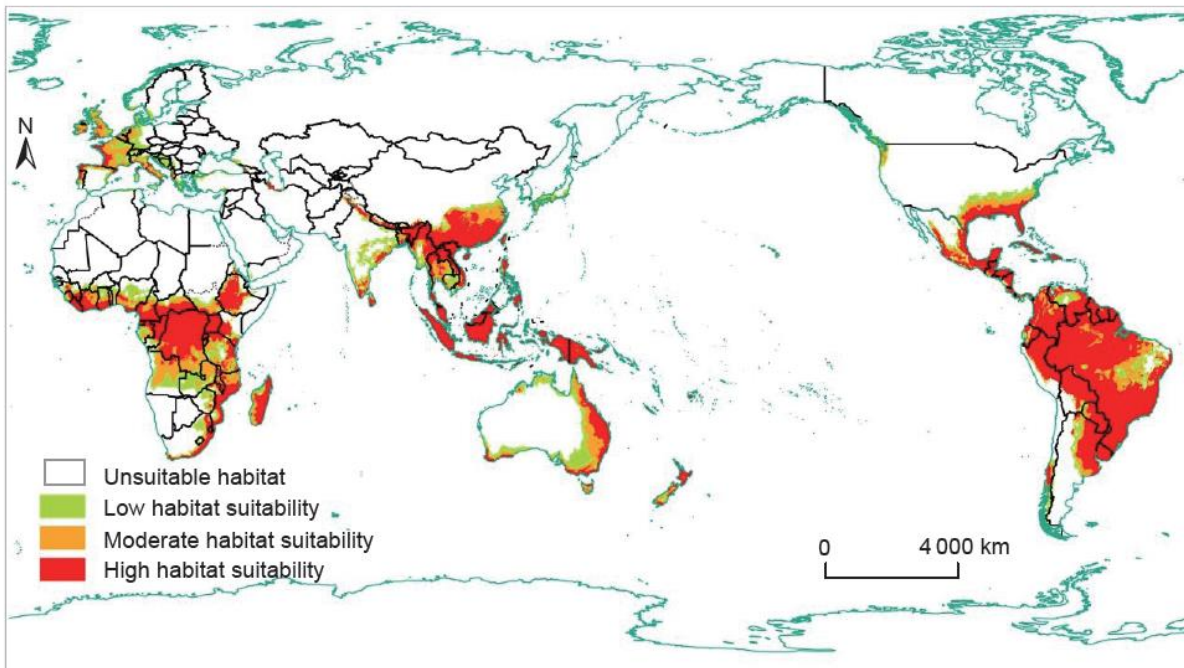
Map inspection number: GS(2020)1908

Figure 3-5. Global habitat suitability map for *Bactrocera neohumeralis*.

3.3.3 Potential distribution of *Bactrocera bryoniae* and *Bactrocera neohumeralis* in China

The projection results showed that south of the Yangtze River region had a wide range of habitable areas for *B. bryoniae* (Figure 3-6). The total suitable area of *B. bryoniae* accounted for 22.06% of the total land area of China. Of the total suitable area of *B. bryoniae*, 11.81, 5.48 and 4.77% had high, moderate and low suitability, respectively. The highly suitable areas for *B. bryoniae* are predominantly distributed in Hainan, Guangdong, Guangxi, Fujian and Taiwan, most parts of Yunnan, southern Jiangxi, Guizhou and Zhejiang, southeastern Sichuan, and some scattered areas in Tibet Autonomous Region. By contrast, the northern Yangtze River region had the smallest habitat for *B. bryoniae* (Figure 3-6).

Compared to *B. bryoniae*, the suitable habitat range for *B. neohumeralis* was slightly larger (Figure 3-7. The total suitable area of *B. neohumeralis* accounted for 22.29% of the total land area of China, of which 14.87, 5.44 and 1.98% had high, moderate and low suitability, respectively. The highly suitable areas for *B. bryoniae* were mainly distributed in Hainan, Guangdong, Guangxi, Fujian, and Taiwan, most parts of Jiangxi, Hunan, Guizhou, Yunnan, eastern Sichuan, most parts of Chongqing, Southern Hubei, eastern Zhejiang, (Figure 3-7). Similar to *B. bryoniae*, northern Yangtze River had and some scattered areas in Jiangsu, Shanghai and Tibet the least suitable area for *B. neohumeralis* (Figure 3-7).
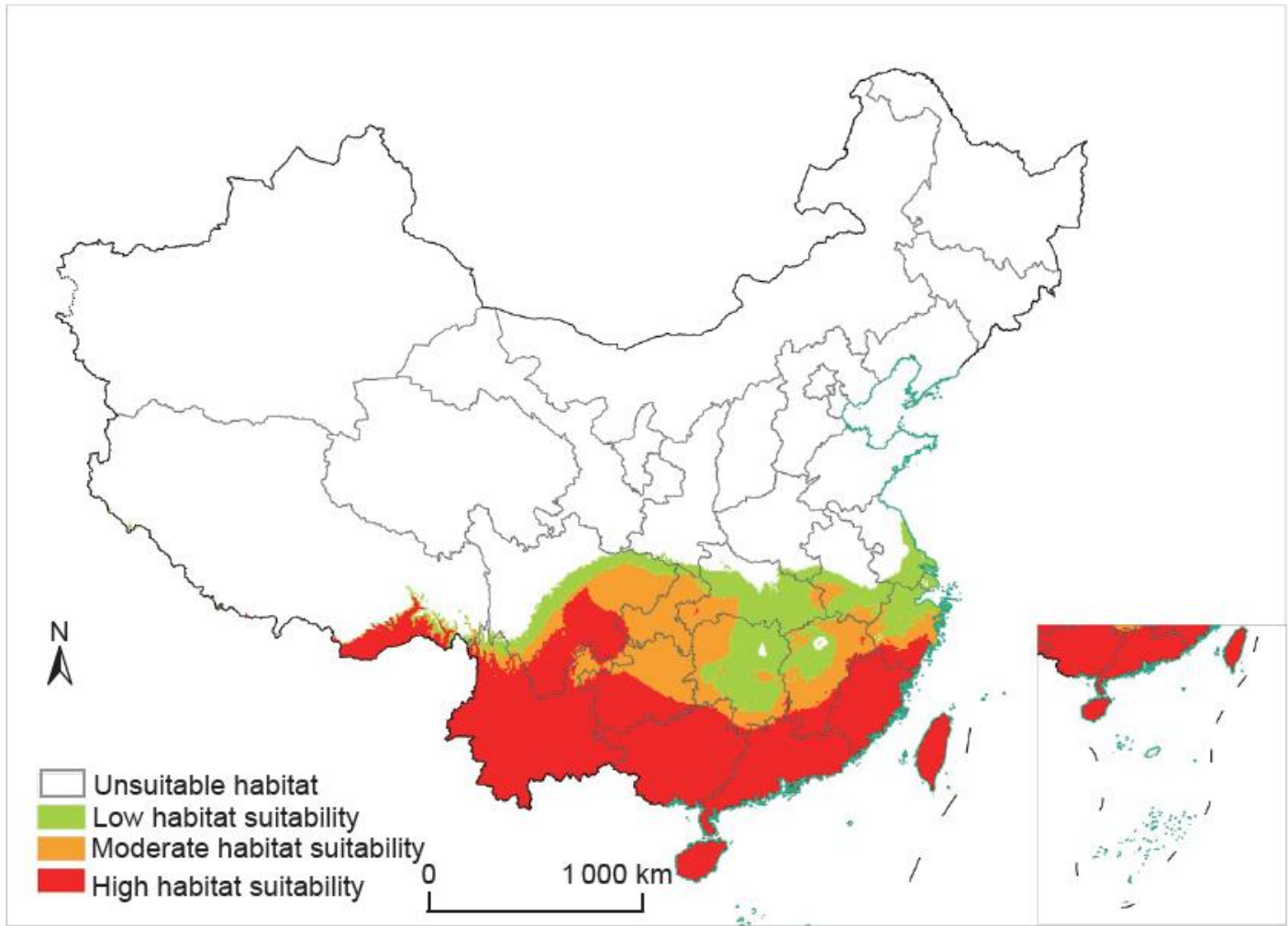
Figure 3-6. Potential habitat suitability map for *Bactrocera bryoniae* in China.
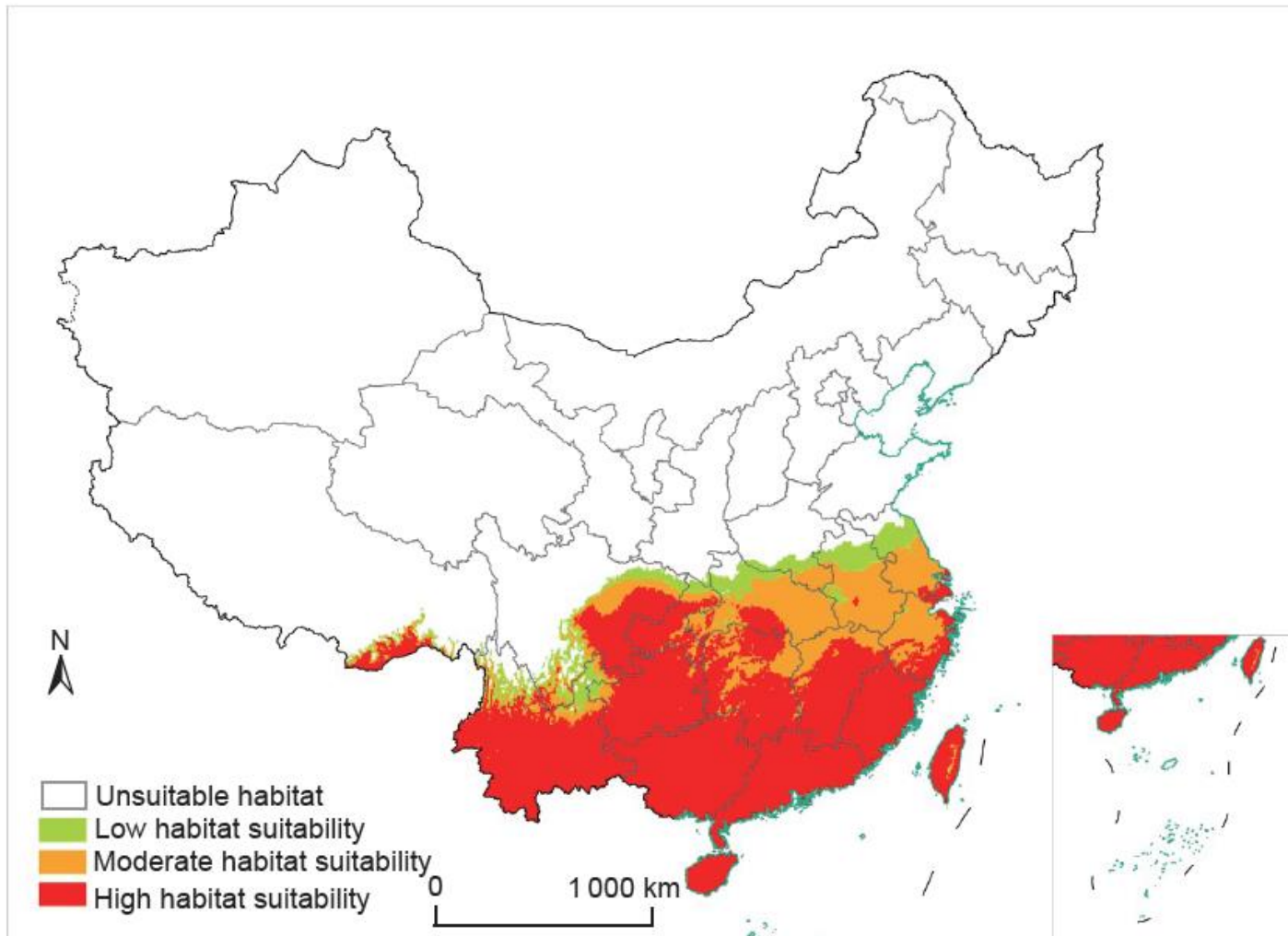
Figure 3-7. Potential habitat suitability map of *Bactrocera neohumeralis* in China.

3.4 Discussion

MaxEnt utilizes continuous and categorical data, incorporates interactions between different variables (Phillips *et al.* 2006), avoids commission errors (Pearson *et al.* 2007), and outperforms other ecological niche models in predicting species distribution (Elith *et al.* 2006; Hernandez *et al.* 2006). We used MaxEnt to predict the potential geographic distribution of *B. bryoniae* and *B. neohumeralis* due to the limited availability of sample localities and the lack of biological characteristic information such as temperature tolerance range. In this study, the MaxEnt model performed well in predicting suitable habitats for *B. bryoniae* and *B. neohumeralis* with AUC values above 0.9 (Figure 3-2), which is referred to as an excellent model-fit category (Phillips and Dudik 2008).

Given their destructive impacts on local commercial fruit and vegetable crops in Australia (Morrow *et al.* 2015; Royer 2015), the risk of *B. bryoniae* and *B. neohumeralis* invasions in the rest of the world must be considered (Zalucki *et al.* 1984; Meats 2006; De Meyer *et al.* 2008). Upon invasion, an invasive species must overcome a series of challenges such as geographic barrier, climate, and natural enemies (Richardson and van Wilgen 2004; De Meyer *et al.* 2010). According to our models, regions with high suitability are more prone to have invasion outbreaks of these fly species. Specifically, southern Asia, the central and southeastern coast of Africa, southern North America, northern and central South America, and the eastern coast of Australia are predicted as highly suitable regions for both *B. bryoniae* and *B. neohumeralis* (Figures 3-4 and 3-5). It is worth noting that the native habitats of *B. bryoniae* and *B. neohumeralis* in Australia were among the predicted invasion areas, reflecting the detection power of our models. Despite the high detection power, this study cannot eliminate the possibility of *B. bryoniae* and *B. neohumeralis* invasions in regions shown negatively in our prediction.

The results of MaxEnt modeling revealed similar distribution patterns of *Bactrocera bryoniae* and *Bactrocera. neohumeralis* in China. However, *Bactrocera neohumeralis* has a wider suitable habitat range comparing with *Bactrocera bryoniae* (Figures 3-6 and 3-7). In China, most areas of the southern Yangtze River are suitable habitats for *Bactrocera bryoniae* and *Bactrocera neohumeralis*. This finding is similar to the potential geographical distribution of the Queensland fruit fly (*B. tryoni*) (Rao *et al*. 2009). Meats (2006) reported a widespread distribution of *Bactrocera bryoniae* and *Bactrocera neohumeralis* in tropical rainforest and subtropical monsoon warm climate in the eastern coast of Australia; thus, increased habitat

suitability of these two fly species across the southern Yangtze River area is likely owing to its similar climatic condition to that of the Queensland fruit fly (Yan 2006; Rao *et al*. 2009). Moreover, southern China has both tropical and subtropical climates and produces a variety of tropical fruits (Qi *et al*. 2015), making it the most vulnerable target of *Bactrocera bryoniae* and *Bactrocera neohumeralis* invasions.

The accuracy of the model depends on the quality and quantity of the occurrence records and the selection of environmental variables (Jiménez-Valverde *et al.* 2011; Qiao *et al.* 2013; Zhu and Qiao 2016). Recent studies suggested that temperature and precipitation have a significant impact on the physiology of fruit fly species (Guisan *et al.* 2013). But Meats (2006) argued that winter field temperatures do not limit the geographical range of *B. neohumeralis*. In Queensland, Australia, *B. neohumeralis* has been reported in areas where the average annual rainfall exceeds 760 mm (Drew 1982). In this study, the MaxEnt model takes into account of temperature, precipitation, and other variables that potentially influence the distribution of *B. bryoniae* and *B. neohumeralis*. Precipitation of the warmest quarter and annual precipitation were the most important among all environmental variables, contributing 68.3 and 46.2% to the prediction of *B. bryoniae* and *B. neohumeralis* distribution, respectively (Figure 3-3). Consistent with this notion, subtropical regions in South and Southwest China, where rainfall is sufficient, were predicted to have an increased fruit fly occurrence. According to these results, precipitation does not seem to be a limiting factor of *B. bryoniae* and *B. neohumeralis* occurrence in South and Southwest China.

Fruit fly pests post a great threat to fruit and vegetable production throughout the world, causing both quantitative and qualitative losses (White and Elson-Harris 1992; Vijaysegaran 1997; Leblanc *et al*. 2012). The most common hosts of *B. bryoniae* include pepper, mango, passionflower, and banana (Liang *et al*. 1998), while similar to *Bactrocera tryoni*, hosts of *Bactrocera neohumeralis* include a wide range of plant species and is highly destructive (Drew 1982; Allwood *et al*. 1999). Consistently, our results show that *Bactrocera neohumeralis* has a higher invasion risk than *Bactrocera bryoniae* by showing a broader host range and a higher climate tolerance. To prevent *Bactrocera neohumeralis* and *Bactrocera bryoniae* invasion, strict inspection and quarantine measures must be enforced at the borders, especially when importing fruits from Australia, New Zealand and the South Pacific regions.

3.5 Conclusions

The results of this study reveal a similar distribution pattern of *B. bryoniae* and *B. neohumeralis* in China and the world. However, in China, particularly the southern Yangtze River area was predicted to be the most suitable for *B. bryoniae* and *B. neohumeralis* survival. Therefore, South China was considered to have the highest risk of invasion. Compared with the potential geographic distribution, the host adaptability and climate tolerance of *B. bryoniae*, *B. neohumeralis* may have high a risk of invasion into these predicted regions.

Chapter Four

Statement of Contribution

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  ➢ The candidate's stated contribution to the publication is accurate (as detailed above).
  ➢ Permission is granted for the candidate to include the publication in the thesis
  ➢ The sum of all co-author contributions is equal to 100% less the candidate's stated Contribution

Name of Co-Author	Rui Wang
Contribution to the Paper	Modelling, Manuscript development, revision, supervision
Overall Percentage	15%
Signature	**Date** 04/11/2020
Name of Co-Author	Yonglin Ren
Contribution to the Paper	Structure format, revision, supervision
Overall Percentage	10%
Signature	**Date** 04/11/2020
Name of Co-Author	Simon McKirdy
Contribution to the Paper	Structure format, revision, supervision
Overall Percentage	10%
Signature	**Date** 04/11/2020

Potential Distribution and the Risks of *Bactericera cockerelli* and Its Associated Plant Pathogen *Candidatus Liberibacter Solanacearum* for Global Potato Production

Abstract

The tomato potato psyllid (TPP), *Bactericera cockerelli*, is a psyllid native to North America that has recently invaded New Zealand and Australia. The potential for economic losses accompanying invasions of TPP and its associated bacterial plant pathogen *Candidatus Liberibacter solanacearum* (CLso), has caused much concern. Here, we employed ecological niche models to predict environments suitable for TPP/CLso on a global scale and then evaluated the extent to which global potato cultivation is at risk. In addition, at a finer scale the risk to the Australian potato acreage was evaluated. A total of 86 MaxEnt models were built using various combinations of settings and climatic predictors, and the best model based on model evaluation metrics was selected. Climatically suitable habitats were identified in Eurasia, Africa, South America, and Australasia. Intersecting the predicted suitability map with land use data showed that 79.06% of the global potato cultivation acreage, 96.14% of the potato production acreage in South America and Eurasia, and all the Australian potato cropping areas are at risk. The information generated by this study increases knowledge of the ecology of TPP/CLso and can be used by government agencies to make decisions about preventing the spread of TPP and CLso across the globe.

4.1 Introduction

In recent decades, there has been ever-increasing concern about biological invasions that pose large threats to food safety, biodiversity, and human activities (Hulme *et al*. 2009; Seebens *et al*. 2017). Invasions of agricultural pests are particularly problematic because increasing global and regional trade of plant products can facilitate their introduction and spread (Desneux *et al*. 2010; Paini *et al*. 2016). Billions of dollars in economic losses have resulted from agricultural pest invasions worldwide (Bacon *et al*. 2014; Teulon *et al*. 2009).

The expanding distribution of psyllids globally over recent decades demonstrates how biological invasions have the potential to cause adverse impacts on natural and agricultural environments (McNeill *et al*. 2006; Munyaneza 2012). Psyllids (Hemiptera: Psylloidea), also

called jumping plant lice, comprise many species that are important crop pests (Syfert *et al*. 2017; EPPO, 2013). Psyllids damage plants both through feeding, which negatively affects plant growth, as well as acting as vectors of many plant pathogens (Salazar 2006; Weintraub and Beanland 2006; Grafton-Cardwell *et al*. 2013; Martini *et al*. 2015). Psyllids can be found in almost all regions of the world where solanaceous crop plants are grown, and in some regions, psyllid pests have caused severe economic losses with almost complete crop failure (EPPO, 2013). In addition to direct losses from crop failure and pest control costs, psyllids can also cause indirect losses such as a decline in agricultural exports due to biosecurity restrictions from importing countries (Thomas *et al*. 2011).

There is much concern regarding the invasion and spread of the tomato potato psyllid (TPP), *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), in Australasia, which includes Australia and New Zealand. TPP is native to Central and North America and has been identified as one of the most destructive solanaceous crop pests. In recent decades, TPP has been found to transmit the Gram-negative bacterium *Candidatus* Liberibacter solanacearum (CLso), which is a pathogen that results in severe yield and quality losses, primarily in potatoes and carrots (Thomas *et al*. 2011; Vereijssen *et al*. 2018; Vereijssen 2020). It has been shown that the distribution of CLso in New Zealand and the Americas follows the dispersion of its psyllid vector, TPP (Munyaneza 2012). CLso was reportedly introduced into New Zealand along with TPP from the western USA in the early 2000s through the horticulture trade. By the time CLso was first recorded in New Zealand, it had already spread to both the North and South Islands (Vereijssen 2020, Gill 2006). Introduction of TPP into new regions is likely to lead to the rapid spread of its associated plant pathogen CLso (Vereijssen 2020). This indicates that the TPP and CLso insect–pathogen complex has enormous potential to expand toward other geographic regions of the world where habitats are favorable.

Tomato potato psyllid is a polyphagous insect that feeds on plants from more than 20 families, with a preference toward solanaceous crops (i.e., potato, tomato and eggplant) and solanaceous weeds (i.e., nightshade) (EPPO, 2013). In view of the wide availability of host plants, the risk of the global dispersion of TPP should be given priority consideration, particularly in regions where economically important crops such as potato and tomato are grown in large areas. The invasion and spread of TPP coupled with CLso may result in serious economic losses in these regions, and even endanger food security. For instance, the economic impact of TPP in the 4

years it has been in New Zealand is estimated in the millions of dollars in terms of increased management costs, crop losses and loss of export markets (Teulon *et al*. 2009). Additionally, there is growing concern about the environmental impact resulting from increased use of chemical pesticides (Teulon *et al*. 2009). For this reason, mapping the invasion risk areas to reveal the likely spatial variation of TPP and CLso and the potential consequences of invasion is imperative.

Ecological niche models (ENMs) are increasingly being applied to risk analysis of invasive pests because of their capacity to predict suitable habitats for pest colonization, allowing the adoption of biosecurity measures to prevent the invasion and spread of alien species in areas of concern (Venette *et al*. 2010; Peterson *et al*. 2011). Correlative models are the most commonly used method to predict the potential distribution of pests in a novel environment. This method connects species empirical observation data with bioclimate data to create a suitability gradient that can be projected onto a geographic space to generate a suitability map (Peterson *et al*. 2011). Additionally, a recent study revealed that psyllid population dynamics were strongly mediated by climate and landscape factors (Gutierrez *et al*. 2020). Here, ENMs coupled with spatial analysis were employed to investigate the potential risk of TPP and its associated plant bacterial pathogen CLso spreading around the globe. First, we compared the climate niche similarity between native and invasive populations of TPP and CLso using bioclimate data for their known sites of occurrence. Then, we employed correlative ENMs to forecast the suitable habitats available to TPP and CLso and produced a potential distribution map. Finally, by coupling ENMs with spatial analysis, we assessed the area of global potato cultivation and at a finer scale Australian potato production to determine the risk of establishment by the TPP and CLso insect–pathogen complex. Together, this information will be valuable for making decisions about how to prevent/address the invasion and spread of TPP/CLso to suitable regions. In particular, this research focuses on the vegetable/potato planting areas of Australia.

4.2 Materials and methods

MaxEnt (version 3.3.3k) (Phillips *et al*. 2006) was selected to build the ecological niche models (ENMs) because it has been shown to be effective in predicting the potential distribution of invasive alien pests when utilizing present-only data (Marchioro 2016; Estay *et al*. 2014).

Building models with proper complexity is crucial to prevent overfitting or under fitting, and to make robust inferences (Warren and Seifert 2011; Merow *et al*. 2013). To build an optimal model for our target species, we optimized the following steps: (i) collecting and spatially filtering occurrence data; (ii) delimiting the background study area; (iii) Comparing the occupied climate space between native and invasive populations; (iv) selecting climate variables; and (v) configuring MaxEnt parameters (regularization multiplier, feature classes) and selecting the best model.

4.2.1 Occurrence data collection and spatial filtering

Occurrence records of TPP and CLso were collated from the literature, the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/), the European and Mediterranean Plant Protection Organization Global Database (EPPO, https://gd.eppo.int/), and a report of occurrences in Australia (https://eldersrural.com.au/wp-content/uploads/sites/3/2017/03/) (DAFWA, 2017). When only locality names were available, georeferenced coordinates were gained with the geolocation software Google Earth. To check and reduce spatial biases, these geo-referenced occurrence points were then subjected to spatial filtering to rarefy the points with a minimum distance of 50 km between each point (Marchioro 2016; Boria *et al*. 2014). This spatial filtering analysis was executed using SDMtoolbox (Brown, 2014) and resulted in 114 unique localities for TPP, of which 81 points were from the native regions in Central and North America and 33 points were from invaded regions in Australia and New Zealand. Similarly, 44 geo-referenced localities were collected for CLso, 21 of which were from the native areas in North America and 13 were from invaded regions in New Zealand.

4.2.2 Background study area delimitation

MaxEnt, like other correlative ENMs, generates pseudo-absence points randomly sampled from the background area (Marchioro 2016; Elith *et al*. 2011). Previous studies indicated that background delimitation is a crucial step during the modelling process and can be achieved using different proxies (Marchioro 2016; Estay *et al.* 2014; Phillips and Dudik 2008). Here, we selected the background study area by intersecting the occurrence localities with Köppen climatic zones downloaded from CliMond (http://www.climond.org) as this approach has been shown to be effective for other pests and is less arbitrary than defining a convex that encompasses all occurrence points (Marchioro 2016; Elith *et al*. 2011; Hill and Terblanche 2014). The climatic zones with at least one occurrence record were selected as background

(Figure 4-1). Random points were generated from the backgrounds to compare the climate niche similarity between invasive and native populations using SDMtoolbox (Brown 2014).
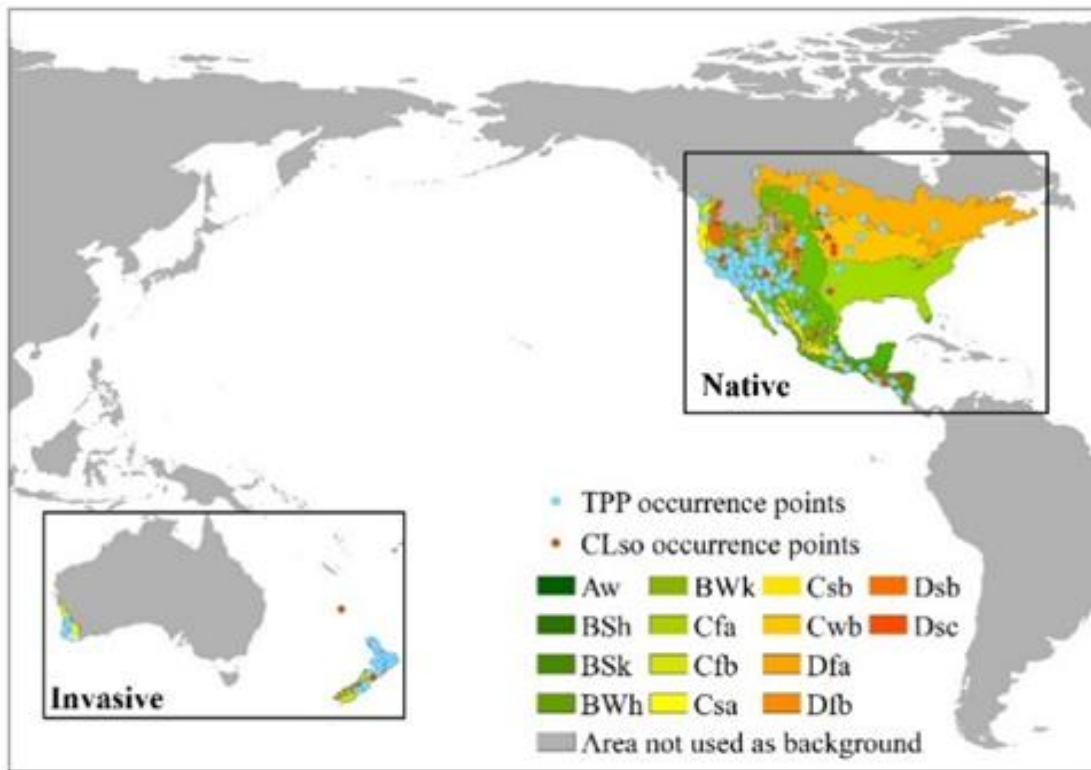
Figure 4-1. Occurrence points and delimited background for native and invasive populations of *Bactericera cockerelli* (TPP) and *Candidatus* Liberibacter solanacearum (CLso). Colors refer to the Köppen climate zones, and gray represents non-target background. Letter codes refer to climate classification: **A**, equatorial; **B**, arid; **C**, warm temperate; **D**, snow; **W**, desert; **S**, steppe; **a**, hot summer; **b**, warm summer; **c**, cool summer; **f**, fully humid; **h**, hot arid; **s**, summer dry; **w**, winter dry.

4.2.3 Occupied climate space comparison between native and invasive populations

When a MaxEnt model is applied to predict the potential distribution of an alien species in a new range, the assumption that an alien species can maintain its climate niche in the invaded regions needs to be validated because the realized climate niche of alien species might shift during the invasion process (Broennimann *et al*. 2007; Broennimann *et al*. 2008; Tingley *et al*. *2014*). Here, we carried out a principal component analysis (PCA) using the values of

occurrence and random points extracted from 19 bioclimatic variables to analyze the climate niche similarity between native and invasive populations of TPP and CLso. A biplot was plotted with the first two components of PCA, and convex envelopes defining clusters of the invasive and native populations of TPP and CLso were added to visualize their climate niche overlap (Hill and Terblanche 2014). The bioclimatic variables were downloaded from the Worldclim database version 2.0 at a spatial resolution of 5 arcmin (http://www.worldclim.org) (Fick and Hijmans 2017). These Worldclim bioclimatic variables were employed to assess climate conditions because they include the climatic factors that determine species' geographic distributions (Guisan *et al*. 2017; Slater and Michael 2012).

4.2.4 Climate variable selection

Previous studies have shown that climate variable selection is an important step for model fitting (Sheppard 2013; Barve *et al*. 2011). Here, two sets of variables were selected following the procedure suggested by Marchioro (Marchioro 2016). The first set of bioclimatic variables (Bio1, Bio2, Bio8, Bio12, and Bio15) was selected based on previous distribution modeling and life cycle adaption studies of other psyllid species (Syfert *et al*. 2017). The second set of bioclimatic variables was determined by adding the Bio14 variable to the first set according to PCA. We also calculated Pearson's correlation coefficients using ENMtools software (Warren and Seifert 2010) to make sure that there was no multicollinearity between the selected variables (Elith *et al.* 2010).

4.2.5 MaxEnt parameter configuration and best model selection

Recent studies have shown that using the default automatic configuration of MaxEnt may not always be appropriate (Marchioro 2016; Merow *et al*. 2013; Phillips and Dudik 2008). It is recommended that the most appropriate model should be selected by evaluating the best potential combination of parameters (regularization multiplier, feature classes) (Warren and Seifert 2011; Shcheglovitova and Anderson 2013; Kumar *et al*. 2015; Morales *et al*. 2017). Thus, we compared models with different feature class and regularization multiplier combinations. MaxEnt includes five basic feature classes: Hinge (H), linear (L), product (P), quadratic (Q), and threshold (T). As simple models with great explanatory predictive power can potentially be produced using various combinations of the feature classes (Shcheglovitova and Anderson 2013; Kumar *et al.* 2015), seven combinations were tested: L, H, LQ, LQP, LQH, LQPT, and LQHPT. The regularization multiplier values were set to 0.5, 1 (default), 3,

5, 7, and 9 based on Marchioro (2016), Kumar *et al.* (2015) and Morales *et al.* (2017). Combining regularization multipliers and feature classes, we assessed a total of 86 models for two environmental datasets, including two default auto-feature models.

Both threshold-dependent and threshold-independent metrics were employed to evaluate model performance. The threshold-independent metrics were the area under the curve (AUC) in a receiver operating characteristic (ROC) plot and the Bayesian Information Criterion (BIC). An AUC value of 1.0 indicates perfect discrimination ability and a value of 0.5 or less indicates a prediction no better than random (Peterson *et al.* 2011). The BIC criterion for model selection measures the trade-off between model fit and complexity, and the model with the lowest BIC is preferred (Warren and Seifert 2011; Radosavljevic and Anderson 2014). The software ENMtools V1.3 was employed to calculate BIC (Warren *et al.* 2010).

Threshold-dependent metrics were the omission rate (OR) at the minimum training presence threshold (MTP) and OR at the 10% training presence threshold (TP10). The expected OR value is 0.1 at the TP10 and 0 at the MTP. Values higher than expected indicate the performance of the model is poor (Boria *et al.* 2014; Muscarella *et al.* 2014). The following criteria were adopted to select the best model with low complexity and high performance: Lower BIC values, OR at TP10 and MTP approximate to 0.1 and 0, respectively, and higher AUC values (>0.8).

4.2.6. Model projection to predict the potential distribution of TPP and CLso

Once the parameter combination yielding the best model was determined, the MaxEnt model was run with all the known occurrences from native and invaded areas and projected onto the remaining parts of the world to predict the potential distribution of TPP and CLso. However, interpretation of model predictions outside the range of the independent variables on which models were calibrated is problematic (Owens *et al.* 2013). A multivariate environmental similarity surface (MESS) implemented in MaxEnt was computed to quantify the extent of the environmental differences between model training and model projection data (Elith *et al.* 2010; Fitzpatrick and Hargrove 2009). To increase the accuracy and reliability of modeling results, the final model was run for 30 replications and output in logistic format. Binary maps showing unsuitable, suitable and optimal habitats for TPP and CLso were then produced using the thresholds MTP and TP10. Habitats with logistic output values less than the MTP were

regarded as unsuitable. In a similar way, habitats with values above the MTP and TP10 were considered suitable, and optimal respectively.

4.2.7 Spatial analyses for quantifying the area at risk of attack

In addition to climate suitability, a recent study indicated that the landscape structure (i.e., host availability) and their spatial arrangement of the host can also determine the occurrence and abundance of pests and thus affect the damage to invaded ecosystems (Gutierrez *et al*. 2020). Here, we further integrated landscape pattern with climate suitability to quantify the area at risk of attack. According to previous studies, TPP and CLso primarily feed on potatoes, tomatoes and capsicums, but can be found on approximately 20 other plant families (EPPO 2013; Vereijssen *et al*. 2018; Vereijssen 2020). As potato is the third most important food crop worldwide, we first quantified the global potato production area at risk of attack by intersecting the TPP suitability map and the global potato distribution map. The global potato production area was obtained from geo-referenced data of potato-producing areas (Schafleitner *et al*. 2011; Hijmans 2001). The acreage at potential risk of attack was calculated using SDMtoolbox with ArcGIS (Brown 2014).

Next, we quantified the area at risk for potential TPP invasion in recently invaded areas of Western Australia by overlapping the TPP suitability map and a national scale land use map of Australia (https://data.gov.au/data/dataset/land-use-of-australia-2010-11). In addition to the cropping and horticulture areas, the residential and farm infrastructure, production forests, and modified grazing pastures were recognized as potential risk areas with available hosts such as backyard tomatoes and solanaceous weeds where TPP is likely to be introduced by unintentional human activities. This is because the new occurrences of TPP in Australia were mainly found in backyards containing tomatoes and eggplants (DAFWA 2017). Previous research also showed that non-crop host plants adjacent to cropping areas are important in the life cycle and ecology of TPP and CLso; this is because the insect's life stages are present year-round and these host plants provide suitable feeding and breeding substrates throughout the year (Vereijssen *et al*. 2018). Similarly, natural conservation areas far from cropping areas can be recognized as risk areas but with low potential of invasion.

4.3 Results

4.3.1 Occupied climate space comparison between native and introduced populations

TPP was found across nine and three Köppen climate zones in its native America and invaded regions in Australasia, respectively. TPP occurred in various climatic zones from tropical to temperate in native regions and only occurred in warm and temperate climatic regions in invaded regions (Figure 4-1). Defining the occupied climate space by PCA allowed us to investigate niche similarity and divergence. The first two principal components of the PCA captured 72.4% of the total variation and these two components were significant. A high degree of overlap between the niches of native and introduced populations of TPP and CLso was observed (Figure 4-2). The available climate spaces in the native and invaded regions form two overlapped clouds, indicating that the available climate space in Australasia is only a part of the occupied climate space in its native habitat in America.
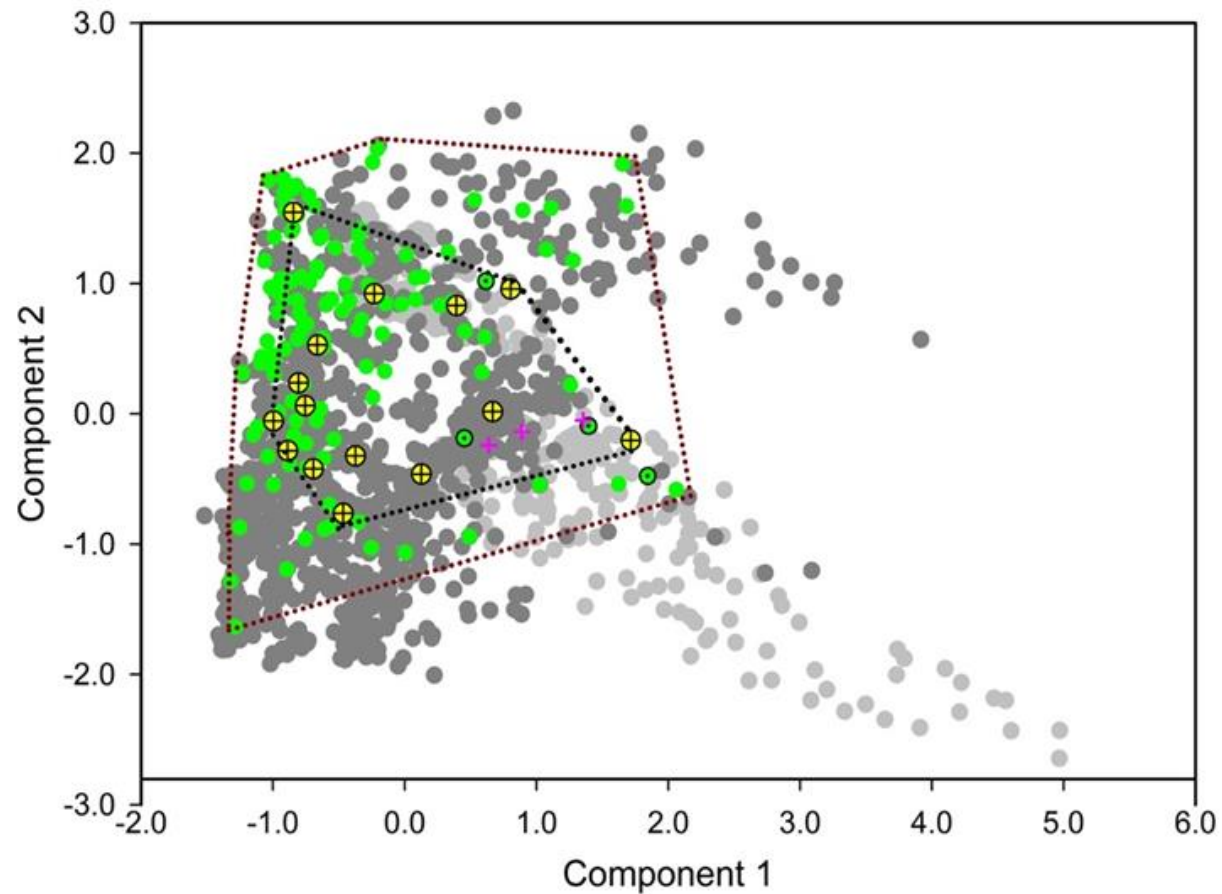
Figure 4-2. Comparison of climatic niches between native and introduced populations using principle component analysis. Green and green dotted circles represent native and invasive populations of *Bactericera cockerelli* (TPP), respectively. Yellow crossed circles and pink plus symbols are native and invasive populations of *Candidatus* Liberibacter solanacearum (CLso), respectively. Light and dark gray dots depict random points generated from invaded and native backgrounds, respectively.

4.3.2 Model calibration and evaluation

Overall, 86 MaxEnt candidate models built with various combinations of regularization multiplier, feature class and climatic variables were evaluated to select the best fitting model to predict the potential distribution of TPP and CLso (Figure 4-3). Both threshold-independent (AUC, BIC) and threshold-dependent (MTP, TP10) evaluation metrics used to assess model performance varied with different parameter combinations. Some models showed ORs close to the expected values, whereas others showed ORs of up to 0.26, almost three times the expected value. AUC values ranging from 0.74 to 0.82 indicated that all models performed better than random. All evaluation metrics changed with different regularization multipliers. The change in the evaluation metrics was nonlinear and generally consistent between the four metrics. The lowest ORs and BIC values and highest AUC values were obtained when the regularization multiplier was 3. Similar trends were seen for different feature classes. The models built with the LQ feature usually had lower ORs and BIC values and higher AUC values. Although the variation in evaluation metrics was consistent between the two climatic sets, the values of evaluation metrics for models built with climatic variables set 2 were subtly higher or lower than those for models built with climate variables set 1. Based on the model selection criteria, the best model was obtained when using L and Q features, a regularization multiplier equal to 3, and climatic variables set 2 (Bio1, Bio2, Bio8, Bio12, Bio14, Bio15); this model had the lowest OR and BIC values, as well as an AUC more than 0.8. The performance of the selected best model was better than that of the MaxEnt model obtained using the default settings (Figure 4-3).
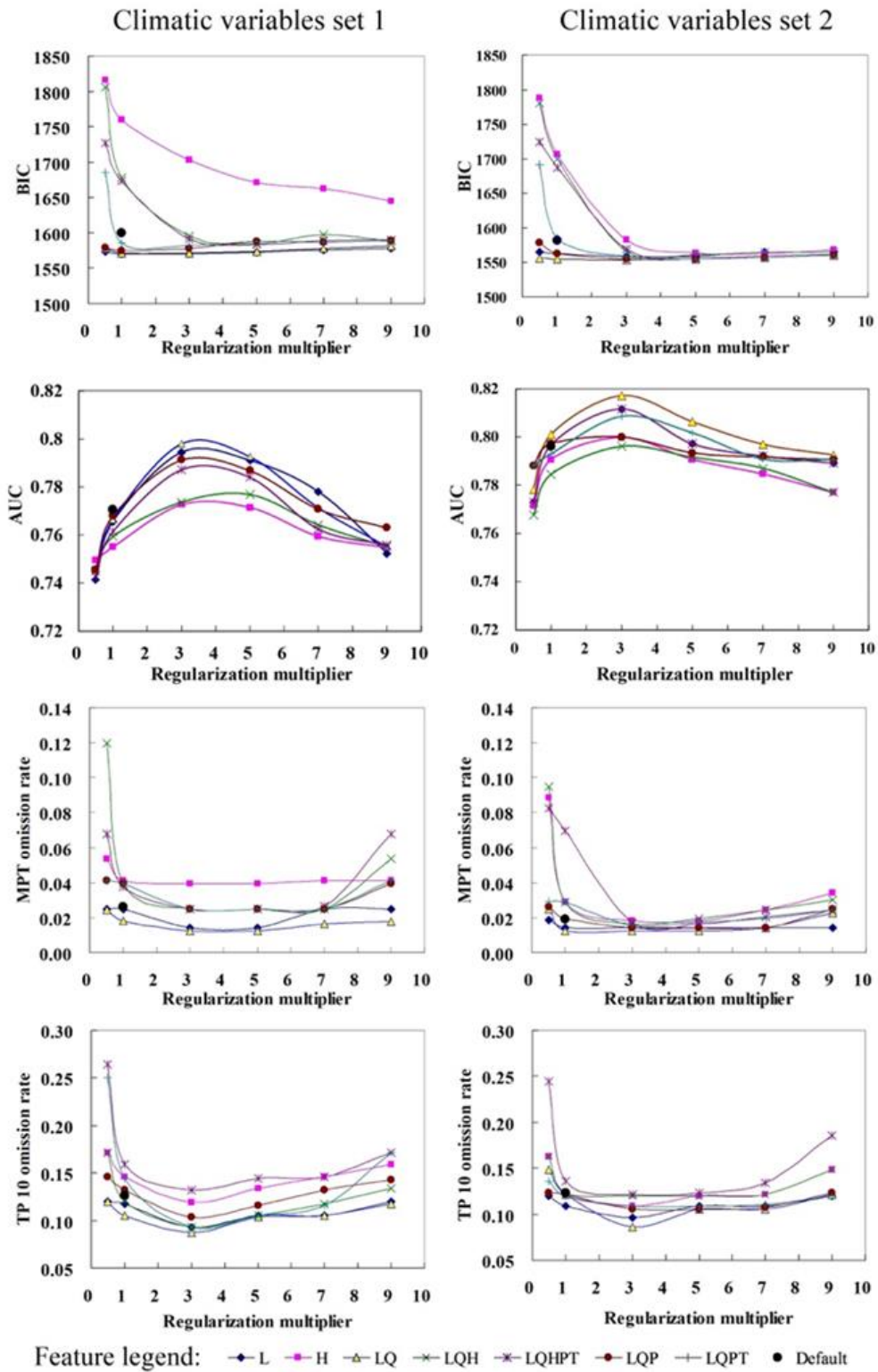
Figure 4-3. Performance statistics for models of *Bactericera cockerelli* (TPP) distribution built with various combinations of regularization multiplier, feature class and climatic variables. (Feature abbreviations: **L**, linear; **Q**, quadratic; **P**, product; **H**, hinge; **T**, threshold).

4.3.3 Potential global distributions of TPP and the bacterial pathogen it transmits

Predicted climatic suitability maps with logistic and binary outputs are shown in Figure 4-4. The suitable and optimal areas were mainly distributed between 47° S and 65° N. In addition to the known regions in Central and North America, four vast climatically suitable and optimal regions were identified in South America, Eurasia and North Africa, sub-Saharan Africa, and Australasia. The optimal areas in South America were in the Andean Highlands and Pampas. The largest optimal area was in Eurasia and North Africa, and largely consisted of regions around the Mediterranean and a belt running from northwestern to southern China and continuing into the Gangetic plains in northern India and Bangladesh. Botswana, Zimbabwe, Southern Africa, Southern Australia, and most parts of New Zealand were also climatically optimal regions.

MESS analysis identified environments that exist in the model's calibrated regions but not in the model's projection areas, and these non-analog environments are shown in Figure 4b. These areas included Mauritania, Mali, Niger, Chad, Sudan, and Southern Algeria in Africa, the Tibet Plateau region in Asia and most regions above 60° N latitude in Europe and North America.
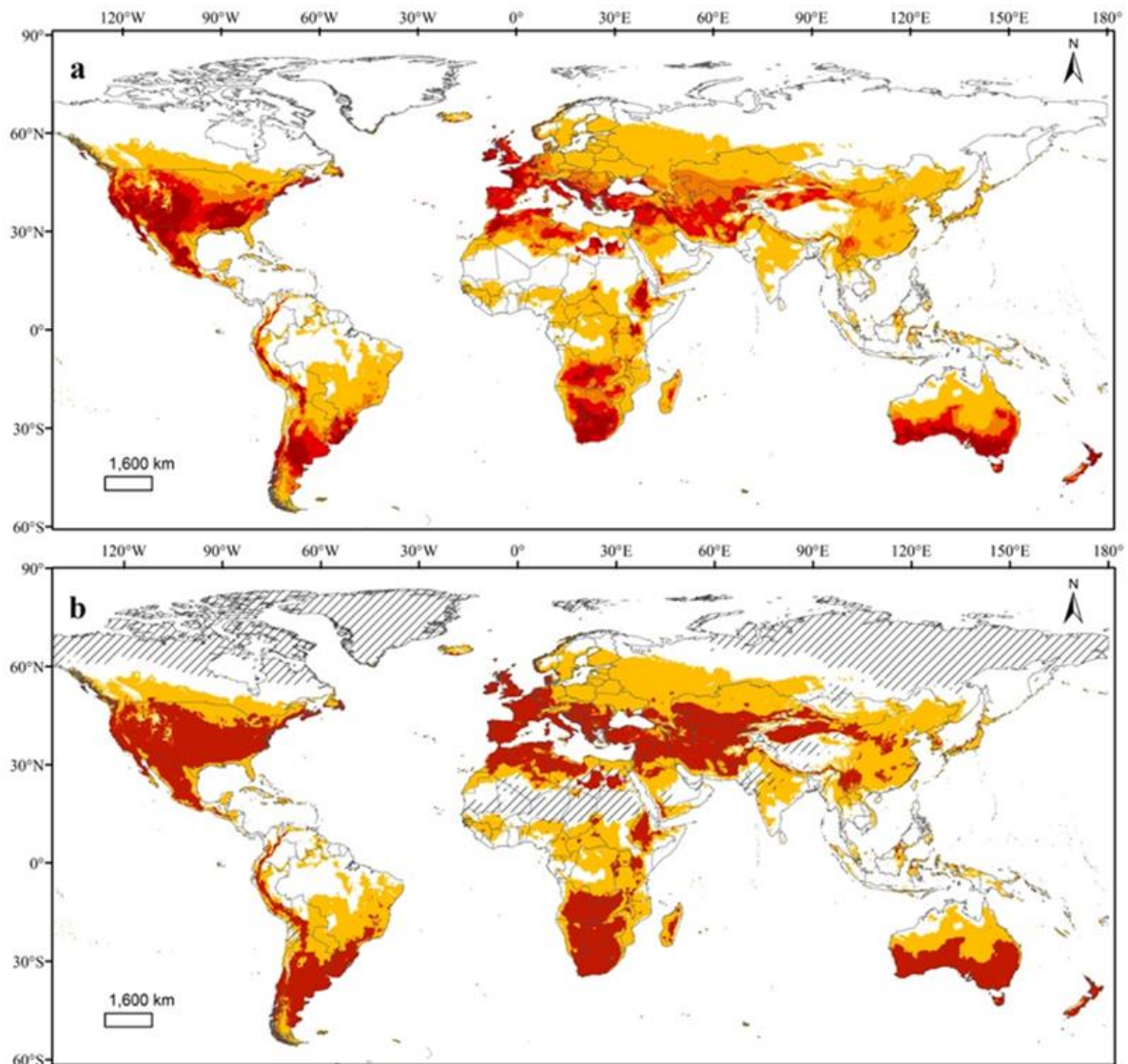
Figure 4-4. Predicted suitable habitats for *Bactericera cockerelli* (TPP) and the associated plant pathogen *Candidatus* Liberibacter solanacearum (CLso) shown as logistic (**a**) and binary (**b**) output. In the logistic map, dark red colors represent higher suitability. Orange and red colors in the binary map represent suitable and optimal conditions for TPP and CLso, defined by the minimum training presence threshold (MTP) and 10% training presence threshold (TP10), respectively. The black simple hatch lines in the binary map indicate the non-analogous environments between the model's calibration and projection areas identified by MESS analysis.

4.3.4 Risks to global potato production and Australian crop production

The predicted suitable and optimal areas for TPP and CLso almost completely overlap with the global potato cultivation area; 79.06% of the known global potato cultivation acreage and 96.14% of main potato production acreage in South America and Eurasia were predicted as both suitable and optimal areas for TPP and CLso (Figure 4-5). The newly invaded areas that are at high risk for potential invasion are located in eastern, western and southern Australia, and include different land use types with host availability. The acreage of Australian lands under risk of attack varies widely between land use types (Figure 4-6). The cropping and horticulture areas are at highest risk, with almost all the area within the optimal range for TPP and CLso, followed by residential, transport and communication areas (97.3%), plantation forest and grazing modified pasture (88.0%), and nature conservation areas (38.67%). The known sites of occurrence in Australia were mainly located in residential regions surrounded by cropping and horticulture areas (Figure 4-6).
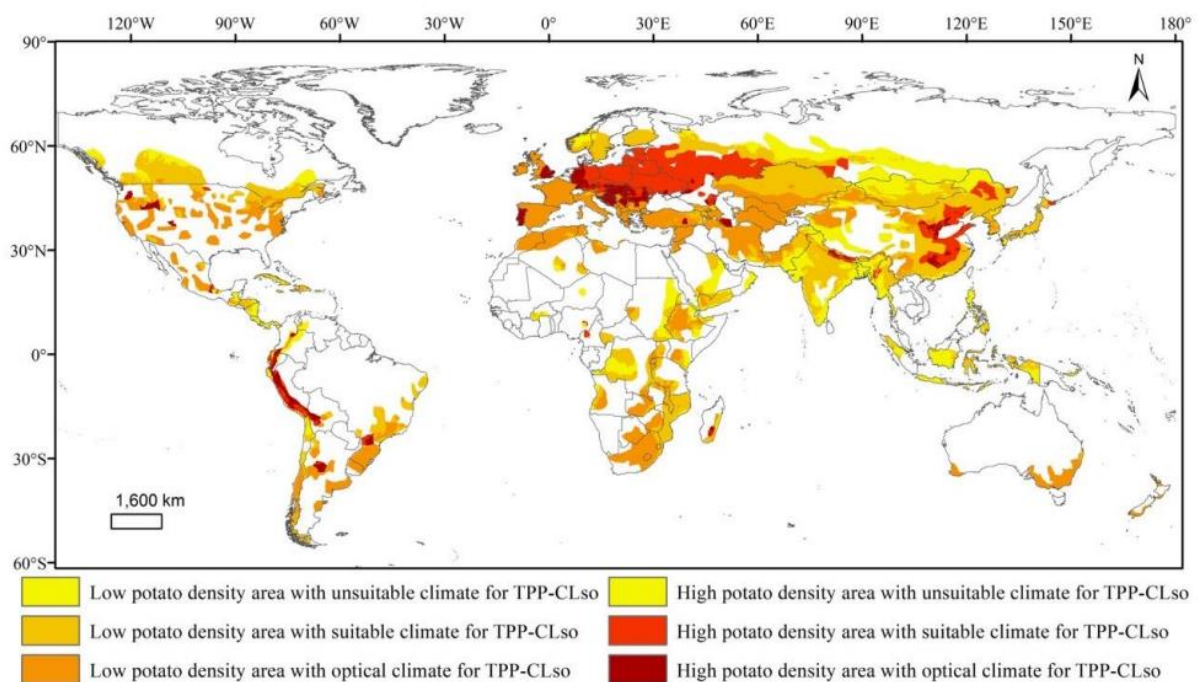
Figure 4-5. Overlap between global potato cultivation areas and predicted climatically suitable area for *Bactericera cockerelli* (TPP) and *Candidatus* Liberibacter solanacearum (CLso).
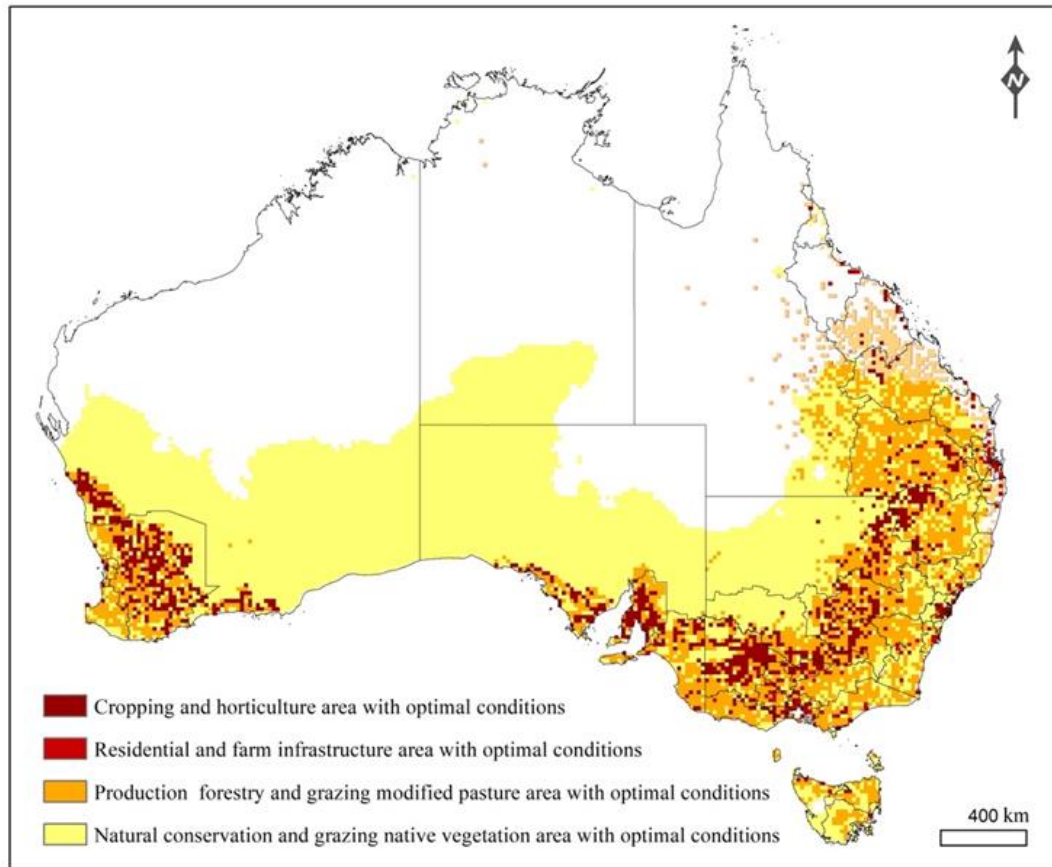
Figure 4-6. Potential areas in Australia at risk for invasion identified by spatial overlay analysis of predicted climate suitability for *Bactericera cockerelli* (TPP) and *Candidatus* Liberibacter solanacearum (CLso) and national scale land use data.

4.4 Discussion

More and more invasive alien pests are being recognized as having an adverse effect on crop production, biodiversity, economies and society (Seebens *et al*. 2017; Paini *et al*. 2016). Quantitative assessment or prediction of the probability of an alien pest invasion and creation of a risk map conveying the spatial variation of a pest is the key to developing strategic and tactical approaches for invasive pest management (Venette *et al*. 2010). Frequently, predicting an invasion is dependent on prediction of climate suitability using extrapolations made from limited information to project how a species might arrive, establish, or spread in novel environments and impact these environments (Venette *et al*. 2010; Peterson *et al*. 2011). In particular, a recent study found that the occurrence and abundance of TPP in its native habitat in the USA could be best described by incorporating climate and landscape factors (Gutierrez *et al*. 2020). Here, we applied MaxEnt models with known occurrence data and spatial bioclimatic layers to predict areas climatically suitable for establishment of the TPP/CLso

complex on a global scale and then combined information about climate suitability from these models with spatial land use layers to assess the risks of invasion in global potato cultivation areas and major crop production regions in Australia that have recently been invaded.

According to the ecological niche model assumption, we evaluated niche conservatism before model calibration (Peterson *et al.* 2011; Broennimann *et al.* 2007; Guisan et al. 2017). No niche shift was found between native and invasive populations of TPP and its associated pathogen CLso. The occupied niches of CLso were found within those of its host TPP and this niche similarity provided us a chance to predict the potential distribution of TPP and CLso as a complex, as it is usually difficult to detect the pathogen (Munyaneza 2012; Gutierrez *et al.* 2020). Niche comparison further indicated that the climate space occupied by the invasive populations is only a portion of that occupied in their native regions, implying that TPP and CLso may continue to expand their range in Australasia unless efficient biosecurity measures are taken.

The performance of 86 candidate models varied largely with changes to MaxEnt's settings. Values of the regularization multiplier had the most impact on model performance, followed by combinations of feature class and climatic variables. Nonlinear variation of model performance with different regularization multiplier values and combinations of feature classes revealed that an appropriate degree of complexity is an ideal property for improving the transferability of ENM models from native to non-native regions when using an ENM model to predict potential distributions, as previous studies indicated (Shcheglovitova and Anderson 2013; Radosavljevic and Anderson 2014; Warren *et al.* 2014; Moreno-Amat *et al.* 2015). Therefore, our results corroborate the findings of other studies (Marchioro 2016; Warren and Seifert 2011; Merow *et al.* 2013; Morales *et al.* 2017; Radosavljevic and Anderson 2014) that it is important to build a MaxEnt model for specific species by testing different combinations of parameters instead of adopting default settings, and that the optimization model should have an appropriate level of complexity.

The final selected climatic suitability model for the TPP/CLso complex revealed four large regions suitable for invasion and establishment in South America, Eurasia, Africa, and Australasia. However, we cannot absolutely infer that TPP and CLso cannot survive in the unsuitable areas because there are some limitations to our predicted potential invasion areas. Our MaxEnt model, built with occurrence data, predicted the realized niche, which is regulated

by both biotic interactions and abiotic factors that shape the species distribution (Peterson *et al.* 2011; Broennimann *et al.* 2007; Guisan *et al.* 2017). Potentially important biotic interactions (competition with local species, presence/absence of natural enemies, population recruitment) were not taken into account due to the lack of relevant information for most psyllid species. Acquiring such information is hindered by the fact that psyllids are small insects and often overlooked in general biodiversity collecting (Syfert *et al.* 2017). Our model projection outside of the native range is thus a relative approximation of the climate niche. It is possible that TPP and CLso could survive in the areas that were predicted as being of low suitability when the amount of the TPP/CLso complex introduced from occurrence regions is high enough. But despite the above drawbacks, the model we built is valuable and informative and provides a fundamental tool for predicting suitable areas for the TPP/CLso complex, revealing areas that are more vulnerable to invasion and establishment than those with unsuitable conditions. Large potentially suitable areas outside its native range suggest that TPP and its associated plant pathogen CLso should be considered an emerging global crop/pest complex.

According to our analysis, substantial portions of Eurasia, South and North Africa, South America, and Australasia were identified as climatically suitable areas with hosts available for TPP and CLso. Most of the host plants of TPP in its native America, including cultivated and wild Solanaceae species, are widely distributed in the predicted suitable regions and may form a plant corridor that promotes the invasion and spread of TPP and CLso. The invasion and spread of this complex to the predicted suitable and optimal regions may cause significant economic losses for local crop producers, because almost all the acreage cultivated with potato, the third most important food crop worldwide, is located within these regions. The use of pesticides to control TPP might also have potential impacts on the local environment and thus increase social costs. It is imperative to formulate biosecurity measures to prevent the global invasion and spread of the TTP/CLso complex, particularly in the newly invaded regions of Australia. Strict quarantine measures, particularly for crop and horticulture products from regions with known occurrence of TPP and CLso, should be adopted for the countries and regions identified as high-risk areas with a suitable climate and hosts available for TPP and CLso.

Although prevention strategies before pests have established viable populations in a novel region is broadly considered more cost-efficient than eradication or control of the invading populations (Lodge *et al.* 2006; Wan and Yang 2016b), not all prevention methods are

effective. This is particularly true in the current globalization era with increasing global and regional communication; even the best prevention efforts cannot stop all invasions of alien species. Early detection coupled with rapid response is a critical second defense against the establishment of newly invaded populations. TPP has already been introduced in New Zealand and Australia, and it is thought to be in the earlier stages of invasion in these regions, which highlights the importance of early detection and rapid response to increase the likelihood that localized newly invaded populations will be found, contained, and eradicated before they become widely established. To increase the probability of detecting established populations, it is important to identify highly vulnerable regions with suitable climates and host plants available for the survival of introduced propagules. Our spatial analysis performed by overlaying suitable areas and land use types delimited the areas at risk for potential invasion in Australia. Nearly all the crop areas and residential areas in Eastern, Southern, and Western Australia are located in the optimal climate regions and thus can be recognized as high-risk areas.

Considering that the currently invaded localities are mainly confined to non-cropping areas (i.e., backyards of residential regions) and that a related study revealed the TPP in its native habitat in the USA was more abundant in landscapes with high connectivity, low crop diversity and large natural areas (Gutierrez *et al*. 2020), monitoring efforts should put more emphasis on the corridors or routes connecting the currently invaded localities and the neighboring crop cultivation regions, particularly those planted with potato and other Solanaceae mono-crops. In summary, the risk maps generated here can be used by biosecurity policy makers and frontline practitioners to delimit priority areas for installing detection traps and conducting field surveys, and to coordinate management efforts strategically and tactically in areas at risk of invasion so as to prevent the invasion and spread of TPP beyond the currently occupied areas as soon as possible.

4.5 Conclusions

Our study highlights the importance of integrating climate and landscape factors using ENM and spatial approaches to identify the areas at risk from invasive pests. Species-specific ENMs should be built with appropriate complexity by configuring the potential parameters to characterize the climate niche and to predict the outbreak of pests across variable landscapes. Large climatically suitable regions with available hosts were identified in Eurasia, South and North Africa, South America, and Australasia. Spatial analysis indicated that predicted suitable

areas highly overlap with global potato cultivation areas: 96.14% of the main potato production acreage in South America and Eurasia, and all the Australian potato growing areas are under potential risk of invasion. Our results and generated risk map can provide scientific guidance for implementing early detection or eradication measures and thus prevent the introduction or spread of TPP and CLso over the globe. In addition, our study contributes to the ecological knowledge of TPP and CLso and could serve as a guide for further experiments to develop novel models for assessing the potential invasion and impact of this pest/pathogen complex.

Chapter Five

General discussion of four invasive pests *Spodoptera. frugiperda, Bactericera cockerelli, Bactrocera bryoniae* and *Bactrocera neohumeralis*

5.1 Biological invasions and the urgent need for risk assessment

Invasive alien species (IAS) are species whose introduction to areas outside of their native range and threat to global biodiversity, economies and human health. In the twenty-first century, the increasing globalization and environmental change, accelerated the biological invasions process. A study has pointed out that one-sixth of the global land surface is highly vulnerable to invasion, including Australia and China (Early *et al*. 2016). According to the research of Seebens, whom stated more than ever alien species saturation problem has become a worldwide phenomenon. In the last 200 years, the annual rate of new first records of alien species has increased, with 37% (a total of 45 813) of them occurring within 50 years (Seebens *et al*. 2017). These IAS cause huge economic loss, with one study estimating the economic costs of invasive insects at a minimum of US$70.0 billion per year globally, as well as over US$6.9 billion per year in health costs (Bradshaw *et al*. 2016). Among all the threatened aspects, the threat to agriculture from invasive insect pests and pathogens, in particular, is most serious. The total invasion cost as a proportion of mean GDP will be as much as 35.7% in some countries (Paini *et al*. 2016). Although Australia is a world leader in biosecurity policy and management with some of the world's most stringent biosecurity, it still suffers from serious biological invasions. There are approximately 429 alien invasive weeds and 80 alien invasive vertebrates that have established wild populations in Australia, which will cause at least $4 billion US dollars annually, while the invasive invertebrates will lead to agricultural production losses of $4.7 billion US dollars annually and cost up $8 billion US dollars annually when considering all impacts and expenses (Hoffmann and Broadhurst 2016). In addition, China has the highest potential losses from invasive insects due to it being the largest food-producing country. There are 560 confirmed invasive alien species, among which, 125 are insect pests, and 92 of these damages the agricultural ecosystem. The estimated annual economic loss due to alien invasive species is more than $18.9 billion US dollars (Wan and Yang 2016).

The best way to reduce the possibility of IAS invasions is to prevent their establishment, which first requires an estimate of the probability of alien species establishment as the potential consequences of that invasion vary spatially, also called pest risk assessment (PRA). The PRA

comprises a set of quantitative and qualitative tools to protect productive ecosystems from the impacts of unwanted biological invasions. There are a number of models and approaches used to achieve this, such as bioclimatic envelopes, habitat models, species distribution models or ecological niche models. CLIMEX the ecological niche model (ENM) is a climate-specific model than can evaluate the suitability of specific regions for target species with consideration to climate change and predict potential pest distribution, with application to climate suitability and seasonal phenology (Byeon *et al*. 2018). The MaxEnt model characterizes the species' known optimal environmental locations through geographically referenced species occurrence data and then links these data with the corresponding environmental data (from the same or different locations) to identify similar sites with optimal environmental conditions (Phillips *et al*. 2006). Unlike CLIMEX, MaxEnt makes it possible to apply environmental variables such as land cover, distance, and geographical factors and to assess the contribution of each variable (Phillips *et al*. 2006). Self-organizing maps is a pedagogy method for pest profile analysis (SOM PPA) designed to assist PRA (Roige *et al*. 2017). It is based on cluster analysis and extracts information out of current distributions of insect crop pests world-wide, allowing the analyst to generate a list of potential risk species for a target region, this model could estimate even thousands of species that have the potential to invade and establish in any particular region or country (Roige *et al*. 2017). In this study, we used the MaxEnt model to estimate the potential distribution of four agricultural invasive insects in Australia or China.

5.2 Risk assessment of *Spodoptera frugiperda*

Several researchers have estimated the potential distributions of *Spodoptera frugiperda* in Australia. Baloch *et al.*, 2020 predicted the potential geographic distribution of *Spodoptera frugiperda* using the MaxEnt model and the ArcGIS with two approaches, Minimum Convex Polygon (MCP) and Observation points (Obs). There are consistent result from these two approaches(Baloch *et al.* 2020). However, some studies have resulted in inconsistent results. A study by Zacarias (2020) also used the MaxEnt to predict the global potential bioclimatic suitability for *Spodoptera frugiperda* and identified that northern Australia is a suitable area for *Spodoptera frugiperda*. Another study estimated the habitat suitability under the present conditions and scenarios of RCP 2.6 and 8.5 (the most optimistic and pessimistic emissions scenarios, respectively), and the result showed that the east coast areas of the USA, the State of Florida, Mexico, Central America, southern part of Brazil, central Africa, and southern Asia

are the high potential habitats of *Spodoptera frugiperda*, while there were low risk of invasions of *Spodoptera frugiperda* into Australia at present and in future (Liu *et al.* 2020).

However, all of the above researchers estimated the potential distribution of *Spodoptera frugiperda* under the global scale. In this study, we also used the MaxEnt to estimate the potential hazard regions for *Spodoptera frugiperda* during different seasons in Australia. Our results showed that in the coldest season, *Spodoptera frugiperda* were restricted to parts of northern Australia. In the warmest season, seasonal populations of *Spodoptera frugiperda* spread southward into most regions of Australia except the central Australian desert from northern Australia where is the winter breeding source area of *Spodoptera frugiperda*. The FAW's summer hazard area comprised 63.79% of the total land area of Australia. Our result is similar to (Zacarias 2020), showing that once the *Spodoptera frugiperda* invades Australia, northern Australia will become a year-round area, and is the most suitable potential distribution region. In fact, until May of 2020, *Spodoptera frugiperda* has invaded 11 regions of Queensland, three regions of the Northern Territory, and three regions of Western Australia (https://gd.eppo.int/taxon/LAPHFR/distribution), which confirmed our prediction of distribution in this study.

In addition, we also predicted the possibility of migration of *Spodoptera frugiperda* to Australia by monsoon circulation using a HYSPLIT atmospheric trajectory model. Our results showed that *Spodoptera frugiperda* could migrate from Kupang and Indonesia to invade northern Australia only in the Northern Hemisphere winter and showed a pattern of predominantly easterly wind-directed trajectories from May to October. Our results tally with the actual situation, that *Spodoptera frugiperda* was first found in the islands of Saibai and Erub, in the Torres Strait, which is situated north of the Australian mainland (https://gd.eppo.int/taxon/LAPHFR/distribution).

5.3 Risk assessment of *Bactericera cockerelli*

Bactericera cockerelli, is a psyllid which is native to North America and has recently invaded Australia. This pest will cause severe economic losses as well as complete crop failure, due to its direct feeding damage and indirectly due to the associated bacterial plant pathogen *Candidatus* Liberibacter solanacearum (CLso) if it is detected in Australia. In this study, we selected ecological niche models of MaxEnt to perform the PRA analyze for TPP/CLso on a

global scale. The result showed that the regions including Eurasia, Africa, South America, and Australasia (Australia and New Zealand) which compose 79.06% of the global potato production acreage are climatically suitable habitats for *Bactericera cockerelli*. Among that, 96.14% of the potato production acreage in South America and Eurasia, as well as all the Australian potato production regions are under the invading risk of *Bactericera cockerelli*. This is similar to another potato Psyllid, the South American Potato Psyllid *Russelliana solanicola*. Syfert *et al.* used the species distribution models (SDMs) to predict the potential establishment of *Russelliana solanicola* worldwide, the result showing that the regions including western South America, Mexico, southern and eastern Africa, central and south-eastern Asia, and southern Australia that grow potatoes are climatically suitable for *Russelliana solanicola* (Syfert *et al.* 2017).

In addition, we also evaluated the potential invasion risk of *Bactericera cockerelli* in Australia. The result showed that the eastern, western and southern Australia are at high risk for invasion of *Bactericera cockerelli*. It is worth noting that South Australia produce 80% of the country's potatoes, with an average production of 2.8×10^5 tons. With more than 11,900 hectares under cultivation, the industry consists of 100 potato businesses (https://www.potatoessa.com.au/industry/growing-regions.html). The invasion of TPP will result in a serious economic loss, which suggests the government should strengthen inspection and quarantine as well as prevention and control for TPP.

5.4 Risk assessment of *Bactrocera bryoniae* and *Bactrocera neohumeralis*

In this study, we also used the MaxEnt model to perform the PRA of two highly destructive and major biosecurity/quarantine pests of fruit and vegetable, *Bactrocera bryoniae* and *Bactrocera neohumeralis*. The result showed that countries including southern Asia, the central and the southeast coast of Africa, southern North America, northern and central South America, and Australia are under invasion risk. Moreover, the eastern coast of Australia is predicted as a highly suitable region for both fruit fly species, which includes their native habitats. Qin *et al.* (2015) used a self-organizing map (SOM) to estimate the global establishment risk of economically important fruit fly species, the result showing that Australia and China will be exposed to a similar risk of *Bactrocera*. In our study, we found that most of the southern Yangtze River area was suitable distribution regions for these two-fruit fly, while southern China was considered to have the highest invasion risk. Considering that South China is the

main fruit production area in China, our result suggests that China will suffer severe threat of these two species, the inspection and biosecurity/quarantine measures should be developed to prevent and control these invasions.

5.5 Some suggestions for biological invasions research

5.5.1 Improving early warning system and monitoring technology

Prevention first is the most important principle of biological invasion control. Therefore, risk assessment and early warning plays an important role in biological invasion prevention and control system. Pest risk assessment (PRA) refers to the quantitative assessment of the impact and loss that affect people's life, property and other aspects after the occurrence of corresponding risky events. There are many PRA models such as Generalized Linear Model (GLM), Generalized Additive Model (GAM), Bioclimatic Prediction System (BIOCLIM), Climate Change Experiment (CLIMEX), Genetic Algorithm for Rule-Set Production (GARP), and Maximum Entropy (MaxEnt) which are based on machine learning algorithm have been employed in predicting the potential distribution geographic region (Baloch *et al.* 2020; Byeon *et al.* 2018; Phillips *et al.* 2006; Qin *et al.* 2015; Roige *et al.* 2017).

Image recognition by deep learning has good performance in monitoring alien invasive plants (Qiao *et al.* 2020). It provides researchers a new perspective to monitor IAS including invasive alien insects. Multiple apps have emerged based on deep learning to identify FAW (Chiwamba *et al.* 2019a; Chulu *et al.* 2019). A system to automate FAW pheromone trapping has even been developed based on machine learning (Chiwamba *et al.* 2019b). Therefore, it is a great opportunity for us to develop new monitoring techniques based on deep learning.

5.5.2 Research on invasion mechanism

Some IAS, such as FAW has had outbreaks with irregular intervals in its native regions for two centuries, before its successful invasion of Africa and Asia. A similar phenomenon, which is called lag-time, has been found in other invasive species: the Brazilian pepper (*Schinus terebinthifolius*) was present as a restricted ornamental for at least 50 years before its rapid invasion everywhere (Simberloff and Gibbons 2004). Thus, there are some questions as to why these invasive species have long invasion lag times, what facilitated invasion, and how many species have invasion potential? We need to clarify the invasion mechanism to better prevent

and control IAS including FAW. The flood of genomic data provide opportunities for us to reveal their invasion mechanism (Huang *et al.* 2019).

5.5.3 Management for IAS

One important reason for the successful invasion of invasive insects is their rapid development of resistance to insecticides, viruses and other environment stresses (Wan *et al.* 2019). Such as, for the resistance of FAW to transgenic crops, most researchers consider that pyramiding multiple transgenes (in the same plant) is more effective in terms of FAW control and insect resistance management (IRM) than single-gene-based resistance (Horikoshi *et al.* 2016; Huang *et al.* 2014). Similarly, for resistance to insecticides, pesticides should be applied at the recommended rates, intervals, and seasonal totals according to instructions, which were designed to slow down the development of pesticide resistance for the FAW population (Prasanna *et al.* 2018). In addition, the IPM strategy shown in Table 5-1 should be used to achieve this goal.

Table 5-1. Integrated pest management measures for fall armyworm, *Spodoptera frugiperda.*

Management	Methods	Pest stages	Corn growth period
Monitoring & Scouting			
Migration monitoring	Entomological radar, vertical-pointing searchlight-raps	Adult	Whole growth
Light traps	Blacklight	Adult	Whole growth
Pheromone traps	Commercial male trap, 50m interval between two traps, traps hung at a height of 1.5 m above ground	Adult	Whole growth
Sampling	Random sampling of 20 plants in five locations	Egg and larva	Whorl stage
Agricultural control			
Insect-resistant corn	Transgenic/Bt maize varieties	Larva	Pre-planting
Cultural control (Push and pull)	Intercropping with bean or sunflower; Trap cropping with castor plant or young corn plants	Egg	Pre-planting
Mechanical control	Handpicking egg masses and larvae	Egg and larva	Whorl stage
Physical control	Deep plowing to kill pupae in the soil/Placing sand or ash in the whorls	Larva and pupa	Pre-planting / Whorl stage
Biological control			
Enemy insects	**Egg parasitoids:** *Trichogramma pretiosum* and *Trichogramma atopovirilia*, etc. **Larval parasitoids:** *Chelonus insularis*, Campoletis sonorensis and *Cotesia marginiventris*, etc. **Pupal parasitoids:** *Diapetimorpha introit* and *Ichneumon promissorius* **Predators:** *Doru lineare* and *Podisus nigrispinus*, etc.	Egg, larva and pupa	Whole growth
Biopesticides	**Virus:** SfGV and SfMNPV **Fungus:** *Metarhizium anisopliae*, *Beauveria bassiana*, Seed treatment with *Trichoderma* induces defense **Bacteria:** BT **Nematode:** *Heterorhabditis bacteriophora*, and *Heterorhabditis indica*, etc. **Botanical:** *Azadirachta indica*, *Schinnus molle*, and *Phytolacca dodecandra*, etc.	Larva	Whole growth
Chemical control			
Sex attractants	Z7-12: Ac + E7-12:Ac + Z9-14:Ac (0.01:0.01:1.00 mg), or other efficient composite	Adult	Whole growth

Insecticides	A total of 20 insecticides were recommended by Ministry of Agriculture and Rural Affairs, PRC. 《Recommended list of insecticides for emergency prevention and control of FAW》 http://www.moa.gov.cn/govpublic/ZZYGLS/202002/t20200221_6337551.htm	Egg and larva	Pesticide sprays at VT (Vegetative - Tassel) stage afterward

5.5.4 Development of new control techniques of IAS

In recent years, some new techniques have emerged for managing pests, including RNAi, CRISPR/CA9, and nanopesticides. One new technique combines RNAi and a nanocarrier to develop a novel, stable and safe strategy that may greatly improve pest management (Ma *et al.* 2020; Yan *et al.* 2020). For FAW, some scientists have focused on the potential of CRISPR/Cas9 in control programs. Wu *et al*. explored the possibility of using the CRISPR/Cas9 system to modify the abdominal-A (Sfabd-A) gene to explore new control strategy (Wu *et al.* 2018). Jin *et al*. (2019) generated a SfABCC2 knockout strain of FAW using the CRISPR/Cas9 system to provide further functional evidence of the role of this gene in susceptibility and resistance to Cry1F (Jin *et al.* 2019). In addition, one study discussed the prospect of studying ORCO using CRISPR techniques in FAW. Due to the efficiency of targeting specific olfactory genes, it is possible to develop new alternative strategies using insecticides and/or microbial sprays to control FAW (Ayra-Pardo and Borras-Hidalgo 2019).

5.5.5 Global collaboration for biosecurity

IAS, such as FAW, TPP, and fruit fly have serious negative effect on the environment, economy, and human health. With the accelerated development of global trade, these species have become a global issue (Bradshaw *et al.* 2016). There is a strong argument for strengthening global collaboration to improve individual country biosecurity defenses to prevent IAS invasions in order to protect food security, biodiversity and human health. Until now, there are numerous organizations making effort in fighting with biological invasions.

World governments and organizations have acknowledged the importance of prevention, eradication, containment and long-term management of IAS, billions of dollars have poured into researchers to find more efficient and effective measures. There are more than 50 international agreements, guidelines and treaties related to biological invasion, among which the Convention on Biological Diversity (CBD) is the most important international treaty on biological invasion management. Other important conventions or organizations include the International Plant Protection Convention (IPPC) and the World Organization for Animal Health (OIE). There are some agreements for specific alien species, such as Convention on Migratory Species (CMS), also known as the Bonn convention, the African-Eurasian Waterbird Agreement (AEWA), the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), etc. Some are international agreements for specific

ecosystems, such as United Nations Convention on the Law of the Sea (UNCLOS), the Ramsar Convention. As a multilateral trading system, the World Trade Organization, formulates binding principles and regulations through the Agreement on the Application of Sanitary and Phytosanitary Measures (SPS) and believes that national measures should follow international standards.

With the gradual establishment and improvement of international management treaties and organizations, in order to deal with biological invasions more effectively, the International Union for Conservation of Nature (IUCN), the Centre for Agriculture Bioscience International (CABI) and Scientific Committee on Problems of the Environment (SCOPE) formulated the Global Invasive Species Program GISP in 1997, which provided guidance information for the prevention and management of IAS, and constructed law on IAS Guidelines for the legal legislation framework.

The guiding principles of biological invasion management mainly include the Convention on Biological Diversity（CBD）and the Conference of the Parties（COP） guiding principles and precautionary principles. COP guidelines regulate the prevention of IAS, including general principles, prevention, reduce species introduction and mitigation impact.

5.6 Conclusion

In this study, we used the MaxEnt model to estimate the potential invasion risk and the geographic distribution of four invasive alien species, *Spodoptera frugiperda*, *Bactericera cockerelli*, *Bactrocera bryoniae*, and *Bactrocera neohumeralis* for Australia and China. The major conclusion are as follows, and our results suggest that the development of inspection and biosecurity/quarantine measures to prevent and control their invasions is urgently.

Spodoptera frugiperda constitutes a new threat and a significant risk to Australia during all seasons of the year. Model simulations indicate that migratory populations of *Spodoptera frugiperda* from Kupang, Indonesia will invade northern Australia only in the Northern Hemisphere winter.

Climatically suitable habitats of *Bactericera cockerelli* were identified in Eurasia, Africa, South America, and Australasia. Intersecting the predicted suitability map with land use data

showed that 79.06% of the global potato cultivation acreage, 96.14% of the potato production acreage in South America and Eurasia, and all the Australian potato cropping areas are at risk.

Bactrocera bryoniae and *Bactrocera neohumeralis* exhibit similar potential geographic distribution ranges across the world and in China, and each species was predicted to be able to distribute to over 20% of the globe. In China, most of the southern Yangtze River area was found suitable for these species, And Southern China was considered to have the highest risk of *Bactrocera bryoniae* and *Bactrocera neohumeralis* invasions.

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