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From species distributions to climate change adaptation: Knowledge gaps in managing invertebrate pests in broad-acre grain crops



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ABSTRACT

Extensive research has shown that climate change will impact the distribution and outbreak potential of invertebrate pests in broad-acre crops. However, much less attention has been placed on translating these likely changes in pest outbreak frequency into practical management options for growers. Dryland grain production systems are generally predicted to be vulnerable to the effects of climate change. An initial step in understanding changes to outbreak potential of different pests is to describe the spatial distribution of different species and communities. Using a bioclimatic modelling approach, we demonstrate how general patterns of distribution for four major invertebrate pests of Australian dryland grain production systems are likely to be altered by climate change. While such models are useful for predicting the direct impacts of climate change on potential species distributions, they are less useful for assessing pest outbreak frequency from direct or indirect changes. In light of this, we explore different tools that can be used to support adaptive management by farmers to limit the impact of induced pest outbreaks. Primarily, research to increase available information of indirect impacts on the pest species and the communities they interact with, including their natural enemies, is required to extend models of pest outbreak potential. Further, incorporation of pests into global crop models combined with monitoring for existing pests and surveillance for new pests is critical for future pest management decision-making. For natural enemies, generalizations around the impact of climate change and flow on effects for pest control services need to be attempted now. The knowledge of potential management interventions is needed by farmers to support improved management decisions in the short-term, but in some cases will also facilitate adaption to climate change in the long-term.

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1. Introduction

Pest outbreaks in agricultural landscapes are driven by a combination of factors including seasonal pest biology, synchrony of host plant resources in the landscape, asynchrony of natural enemy species that otherwise limit population growth, and management actions that inadvertently facilitate population growth and movement (Letourneau, 2012). These factors are all influenced by climate to some extent. Increases in temperature, greenhouse gases (especially CO₂), and rainfall patterns as a result of global climate change will undoubtedly continue to exacerbate some pest problems in grain crops, and alleviate others. However, the development of management options for farmers to mitigate or adapt to these risks appears slow.

Invertebrates are especially sensitive to climate conditions, and parameters such as temperature, rainfall, relative humidity and soil moisture have proved useful for predicting important events in the growth of pest populations (e.g. Chen et al., 2014; Klapwijk et al., 2012). Changing pest profiles in southern Australia (Hoffmann et al., 2008), earlier spring flights in aphids across Europe (Hulle et al., 2010), destabilization of the outbreak cycles of the multivoltine tea tortrix moth in Japan (Adoxophyes honmai) (Nelson et al., 2013), and earlier arrival across the United States of America (USA) of the potato leafhopper, (Empoasca fabae) (advanced by 10 days over the last 62 years) especially in warmer years (Baker et al., 2015) have all been attributed to climate change. In practice, determining whether such changes are solely driven by climate is challenging, and examples with unequivocal evidence of changes to agricultural pest outbreaks driven solely by climate change are rare. This is because pest outbreaks are typically due to interactions between biotic and abiotic factors (including climate) and management choices (Ali et al., 2014; Li et al., 2015). For

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example, pesticide applications are often applied prophylactically across large areas, so climate induced shifts in abundance and distribution may be obscured (Hoffmann et al., 2008). Ewald et al. (2015) used a 42-year data set to examine historical changes in abundances of a range of invertebrate groups in cereal fields. Whilst some long-term trends in abundance were correlated with temperature and rainfall, pesticide-use was more important in explaining patterns in abundance. We expect that if climate changes lead to an increase in pest outbreaks, farmers may respond by applying more pesticides to minimize the potential of pest damage (Ziska, 2014). It is especially hard to predict the consequences of changes in multiple factors at once (Rosenblatt and Schmitz, 2014).

Determining the likely impacts of climate change on pest invertebrates, and quantifying the consequences of these impacts, is required to provide advice to farmers regarding adaptive responses. Such responses may include changes to pesticide use, improved pest monitoring technologies, better timing and management of insecticide inputs, changes to crop rotation sequences, changes to tillage and stubble retention practices, through to enterprise-wide alterations to land-use. Some of these responses are inexpensive and represent a shift toward more

sustainable pest management practices. Others are costly to implement and have implications for a myriad of other farm business decisions. For example, shifting from one crop type to a different crop type that has a lower susceptibility to pest damage may involve changes to seeding and harvesting equipment, changes to crop rotation practices and changes to buyers and marketing of the grain. Conversely, changing to a different crop variety that allows for earlier or later sowing may require only minimal alterations. It is important to build our capacity to predict the impact of climate change on the likelihood of pest outbreaks as the knowledge-gained through such exercises will aid adaptive management strategies in the future (Sutherst et al., 2011).

Here, we summarise the evidence-base for the potential direct and indirect impacts of climate change on outbreaks of pest species on grain production systems. We use examples from the published literature and models developed for some common pest species in Australia to improve our understanding of the threats posed by existing pest species under future climate change scenarios. The Australian context provides an ideal case study because grain production there is already vulnerable to seasonal rainfall variability along with the added effects of climate change, and the crops are attacked by a range of polyphagous pest species that

Table 1Examples of studies showing three potential responses of pests to changing climate. Examples from studies of invasive species have been included as a surrogate for climate change impacts as these species may experience new climates in their invasive ranges. Also see Table 7.4 in Reddy, (2015); and Table 2 in Juroszek and von Tiedemann, (2013).

Response group	Species	Details	Citation
Shifting distributions	Penthaleus spp. (blue oat mites)	Distributions of the three <i>Penthaleus</i> species in Australia are correlated with different climatic variables, suitable climate space likely to decrease in the future. Cryptic species respond differently.	Hill et al. (2012)
	Leptinotarsa decemlineata, Colorado potato beetle, Ostrinia nubilalis, European corn borer	The models suggest a widening of the area of suitable habitat for both pests in central Europe.	Kocmankova et al. (2011)
	Diabrotica virgifera virgifera, western corn rootworm	The models showed a northward advancement of the upper physiological limit in the Northern hemisphere, which might lead to increased outbreaks at higher latitudes.	Aragón and Lobo, (2012)
	12 pest fruit fly species (Tephritidae)	Results from distribution models revealed general patterns of poleward movement for the group. For individual species, distribution shifts appear to also be eastward, and at finer scales, varying amounts of species turnover was apparent. These changes in response across different scales present regional management challenges for these species under climate change.	Hill et al. (2016)
Altering phenology	Leptinotarsa decemlineata, Colorado potato beetle, Ostrinia nubilalis, European corn borer	Models suggest an increase in the number of generations per year. Area of arable land affected by a third generation per season of L. <i>decemlineata</i> in 2050 is c. 45% higher, and by a second generation of <i>O. nubilalis</i> is nearly 61% higher, compared to present levels.	
	Cydia pomonella, Codling Moth	Under future conditions of increased temperatures (2045–2074) in Switzerland, the risk of an additional third generation will increase from 0–2% to 100% and there will be a two-week shift in earlier overwintering adult flight. The shifts in phenology and voltinism will require change to plant protection strategies.	Stoeckli et al. (2012)
	13 agriculturally important pest insect species.	Degree-day models were used predict the voltinism of 13 agronomically important pests in California, USA. Under future climate change all species are likely to see an increase in voltinism per year, with different climate change models contributing variance across results.	
	Halotydeus destructor (redlegged earth mite)	Models suggest that the temperature cues for post-diapause egg hatch have evolved markedly between the western Australian "Mediterranean" environment (20.5 °C) and the south-eastern Australian (16 °C) more temperate environment.	McDonald et al. (2015)
Adjusting to persist <i>in situ</i> (phenotypic plasticity or adaptation)	Halotydeus destructor (redlegged earth mite)	Species distribution models indicate that invasive populations of <i>H. destructor</i> in Australia have undergone a recent range shift into hotter and drier inland environments since establishing a stable distribution in the 1960s. Experiments measuring physiological traits reported greater thermal tolerance in Australian populations than South African (native).	Hill et al. (2013)
	Zaprionus indianus (African fig fly)	Invasive populations in India display latitudinal clines indicative of rapid adaptive shifts. Traits included in studies were desiccation and starvation tolerance of adults, body weight, wing length and thorax length, and number of ovarioles.	
	Aedes albopictus (Asian tiger mosquito)	Invasive populations in USA from Japan demonstrated rapid adaptive evolution (in 20 years) of the photoperiodic response during invasion and range expansion into higher latitudes. Change in photoperiodism has been an important adaptation to climatic variation across the invasive range.	Urbanski et al. (2012)

display different responses to factors such as temperature and rainfall. We also consider studies that include brassica crops (e.g. canola) as they are commonly used in the cereal rotation in substantial regions of Australia. Finally, we discuss which tools and knowledge farmers currently need to enable more adaptive approaches to managing pests, both in terms of mitigating the likelihood of negative changes occurring in the future, and managing unavoidable changes.

2. Direct effects of a changing climate on pests

Warm and wet conditions favour the growth and development of a range of pest insects, diseases and weed species (Harrington and Woiwod, 1995; Luck et al., 2011; Juroszek and von Tiedemann, 2013; Svobodova et al., 2014) and thus potentially cause large crop losses. There are three ways in which invertebrate pests might directly respond to a warming climate: (i) shifting distributions (mostly poleward) to track favorable temperature and or moisture requirements, (ii) altering phenology, and (iii) adjusting to persist in situ through phenotypic plasticity or evolutionary adaptation (Thomson et al., 2010; Jeffs and Lewis, 2013; Eigenbrode et al., 2015). If the species is biologically or ecologically unable to respond in these ways they may become locally extinct or reduce in abundance to the point at which they are less often considered a pest species. Potential shifts in pest species' distributions, phenology and persistence have been the focus of numerous research studies (Table 1), which have been enabled by the development of a variety of species distribution modelling (SDM) tools. Species Distribution Models take many different forms (Hill and Thomson, 2015), the most prevalent being environmental niche models which are typically based on species occurrence data linked to climate predictor variables (Elith et al., 2006; Kearney and Porter, 2009). By characterising species-environment relationships it is possible to map areas where species are likely to persist. This approach can be extended to predict where a pest species might move to, or be able to persist, under certain climate change scenarios (e.g. Aragón and Lobo, 2012; Meynard et al., 2013), and hence can be a useful tool to assess the direct effects of climate change on a species. Through the case studies below (2.2) we provide examples of how this approach can be used to identify areas in Australia which are likely to experience a changing suitability of climate over time for four important invertebrate pest species.

2.1. Shifting distributions

For pest species in general, there is a common prediction of poleward shifts in distributional limits in relation to climate change (Bebber et al., 2013). Svobodova et al. (2014) used SDMs to estimate the impact of climate change on multiple crop pest species in Europe. Using an ensemble of different climate change

models, the authors describe a projected shift in the species ranges to higher altitudes and increases in the number of generations of pests in central Europe by 2055. However, in southern Europe, the number of generations was expected to decrease due to temperature increases that would negatively affect pest populations. Similarly, pest species' models suggest that in Australia many grain production regions will ultimately become less favorable for the growth and development of some species (Farrow et al., 1993; Hill et al., 2012), however there is geographic variation in where this reduction in risk occurs (see 2.2 case studies). Importantly, the aggregate response of multiple pest species may be different to species-specific responses for instance at the regional level, which can show contrasting or masked patterns to overall trends (Hill et al., 2016).

2.2. Case studies on distributional shifts of Australian grains pests

To demonstrate how direct effects of climate change may result in distributional changes, we considered four important pest species in Australian grains production systems. In Australia, broad-acre grain crops (predominately winter cereals) are grown across a wide geographic area in a number of regions that have different soil and climate characteristics. Bulk-handled grain production businesses have an average annually cropped area per farm of 876 ha (inferred from Thompson, 2015), and often incorporate pastures for livestock as part of the cereal rotation. Other crops (mainly pulses and oilseeds) once used principally as break crops to assist in the management of nitrogen, weeds, diseases and pests, have become increasingly important cash crops in their own right. Climate change projections for Australia suggest an annual temperature increase of 0.6-1.3 °C by 2030 (above the climate of 1986-2005, CSIRO and Meteorology, 2015). The net impact of this change on dryland crop production is likely to be negative (although there is some regional variation, Ghahramani et al. (2015)). More hot days and fewer frosts are projected. The reduction in frost potential will allow some crop varieties to be planted earlier (assuming the rainfall is adequate) and may lead to increased yields in some areas (Zheng et al., 2012). However, there may also be an accelerated crop development rate and this is likely to reduce yields due to the shortened exposure to solar radiation for the plant. Projections about long-term changes in rainfall patterns are more difficult to make with confidence (Howden et al., 2010). However recent models predict less annual rainfall, with the biggest loss during winter/autumn, and an increased chance of extreme rainfall events in summer. This may make planting at the optimal time difficult (Howden et al., 2010). These changes will create opportunities for land-holders in areas of currently high rainfall to devote more land to cropping as their location becomes dryer, and cause some growers to shift away from cropping in the already marginal areas (Ghahramani et al., 2015).

Table 2Summary of the biological and ecological characteristics of the pest species modelled in the cast studies of Australian grain production systems.

Common name	Plutella xylostella diamond-back moth	Helicoverpa armigera corn earworm, cotton bollworm	Halotydeus destructor redlegged earth mite	Rhopalosiphum padi bird-cherry oat aphid
Resident or migrant	long-distance disperser	long-distance disperser	resident (but some human mediated long-distance)	resident and long-distance disperser
Sexual or asexual reproduction	sexual	sexual	sexual	asexual (in Australia)
Diapause	No	Yes, pupal diapause over winter in Queensland (facultative)	Yes, oversummer as eggs (facultative)	No
Number of generations per year	Multiple and overlapping (3-5 per year)	Multiple, 5–4 per year in Queensland	Multiple across autumn and winter	Multiple
Likely native range	UK (but has cosmopolitan distribution)	Unsure	South Africa	Suspected to be from Europe or North America

Losses in Australian grain production systems due to invertebrate pests are currently at least AU\$359 million annually, and pesticide treatments applied to limit damage is valued at AU\$159 million (Murray et al., 2013; Valenzuela and Hoffmann, 2015). Grain crops are attacked by diverse introduced and endemic pest insects and mites, with contrasting life-histories and varying responses to environmental conditions Nash and Hoffmann (2012). We selected four of the most economically costly pest species in Australian grain production systems (Murray et al., 2013) to demonstrate the potential direct impact of climate change on the species' distribution using SDMs. These species, each of them cosmopolitan, have been the focus of previous studies that have published species distribution modeling parameters in Australia for other purposes (Table 2, full methods can be found in Supplementary material A). We generated spatial outputs from CLIMEX (Sutherst and Maywald, 1985; Sutherst et al., 2007), a climate-based modelling program for exploring the relationship between climate, species distributions and geographic locations suitable for the growth of a species (see detailed methods in Supplementary material A). We do not include projections relating to potential future grain crop distributions. The four pest species are polyphagous to varying degrees and use a range of crop and non-crop host plants throughout a wide geographic range. To keep our projections manageable we assume that host plant distribution will not be a limiting factor (as it is not now).

2.2.1. Case studies

2.2.1.1. The diamondback moth, Plutella xylostella. Plutella xylostella (Lepidoptera: Plutellidae) is a widespread pest of brassica crops across Australia. This pest develops under a wide range of temperatures and simply slows or accelerates development at low or high temperatures (Bahar et al., 2012; Dosdall et al., 2012). The number of generations that can be completed per year in Australia vary from three to almost five depending on the seasonal

conditions (Nguyen et al., 2014). The influence of rainfall on development is less clear, with outbreaks recorded after both unusually wet and dry conditions (Furlong et al., 2008). Plutella xylostella does not go into diapause but has the ability to disperse quickly over long distances (Table 3). This means that seasonal recolonisation of cropping regions can be influenced by factors in source regions potentially tens or hundreds of kilometers away (Furlong et al., 2008). It is likely that an increase in temperature will accelerate the development of this species and increase the number of generations per year. However, experimental evidence suggests that extreme high temperatures or longer durations of hot temperatures can be lethal (Nguyen et al., 2014). The CLIMEX models suggest that by 2090 there will be a substantial decrease in the areas suitable for year-round growth and development of P. xylostella across Australia (Zalucki and Furlong, 2008), mainly due to temperatures increases (Fig. 1). However, there are regional differences. In general, areas in the coastal fringe become more suitable, while areas inland and in Northern Australia will become less suitable for this species (Fig. 1).

2.2.1.2. Cotton bollworm, Helicoverpa armigera. In Australia, the caterpillar pest H. armigera (Lepidoptera: Noctuidae) is best known for causing problems in northern cotton crops, but is commonly recorded in all states and on grain crops (Zalucki and Furlong, 2008). In parts of Queensland and northern New South Wales, H. armigera goes into diapause over winter as a pupae under the soil surface, but this diapause is facultative and depends on temperature and photoperiod (Chen et al., 2014) (Table 2). Whilst H. armigera is able to develop under a wide range of temperatures, the survival rate of adults is decreased through a combination of exposure to increasingly higher temperatures (40 °C and above), and increasing duration of exposure (minutes to hours) (Mironidis and Savopoulou-Soultani, 2010). Furthermore, increases in carbon dioxide have been shown to increase the length of the larval stage of H. armigera when fed on wheat (Yin et al.,

Table 3Examples of several management options that a farmer might consider if climate change models suggest their risk from certain pests is likely to increase, decrease or not change. Some of these options are associated with more sustainable pest management under today's climate, regardless of future change in risk. A tick indicates that the management option is suitable given the change in risk profile, *and* the degree of difficulty associated with adoption of the management option. A cross indicates that the management option is unsuitable given both the modelled change in pest risk, *and* the degree of difficulty associated with adoption.

Management option		Modelled change in pest risk		Degree of difficulty ^a
	Risk reduced	Risk increased	No change (or not sure about direction)	annearcy
Change planting time to avoid period at which crop is susceptible.	X	~	X	2
Change planting density or row spacing to make micro-climate less favourable.	/	/	~	1
Change seeding density to compensate for early plant loss.	X	✓	∠	1
Change crop variety, consider those less susceptible to damage (and better adapted to local climate conditions).	~			1
Change crop choice, consider those not a host for pest (and better adapted to local climate conditions).	X		X	3
Change in-field weed control to reduce alternate plant hosts.	X	✓	X	2
Gradually reduce insecticide-use, and monitor for frequency of outbreaks.	/	X	~	1
Use forecasting tools/monitoring networks to help decide when and where to scout, and then make spray decision.	X		X	2
Use border sprays only.	/	X	X	1
Manage weed growth surrounding the field.	X	/	X	2
Use strategic tillage to reduce stubble that provides an ideal micro-climate for some pests.	/	X	~	2
Use conventional tillage.	X	_	X	1
Improve pest and natural enemy identification skills. Understand the non-target impact of pesticides.	~		"	1
Employ an agronomist to help with pest management decisions.	X	_	X	2
Establish a support network of neighbours, agronomists and researchers to help when new pest issues arise.	~		-	1
Increase crop diversity at the whole-farm level.	X	/	X	3
Increase plant diversity at the whole-farm level.	X	/	X	3

^aThe management change may be costly or complex to implement. 1, not difficult to implement; 2, moderately difficult (i.e. will require small changes in other areas of farm business, has small costs); 3, very difficult to implement (i.e. will require large changes in other areas of farm business, is costly and difficult to go back).

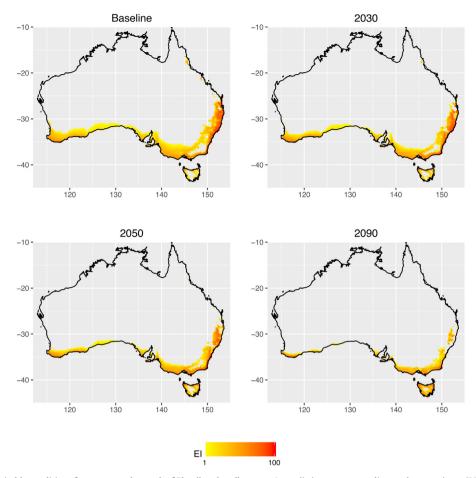


Fig. 1. The change in the suitable conditions for year-round growth of *Plutella xylostella* across Australia in response to climate change using a CLIMEX model for this species. Each model projection is shown as the Ecoclimatic Index (EI) ranging from 1 to 100. One scenario (A2) is shown and the consensus areas as an average between two Global Climate Models (CSIRO Mk3.0 and the Miroc-H) for the time periods 2030, 2050 and 2090.

2009). The CLIMEX model (Kriticos et al., 2015) shows that parts of southern Australia are becoming more suitable for this species, and the areas in northern Australia (especially along the coast) are becoming less suitable by 2090 (Fig. 2). The areas suitable for growth and development constrict to the coastal areas, disappear from northern Australia, and are more focused in southern Australia and Western Australia.

2.2.1.3. Redlegged earth mite, Halotydeus destructor. Halotydeus destructor (Acari: Penthaleidae) is a widespread mite pest in both pastures and crops at the establishment phase, especially canola. It is active in autumn and winter during the cool and wet months, after hatching from diapausing eggs (Table 2). A significant rainfall event and period of cooling temperatures triggers egg hatch (McDonald et al., 2015). Given the requirement of this species to produce diapausing eggs over summer we would expect that changes in both temperature and rainfall will greatly impact the population dynamics of this pest. Experimental studies have shown that mortality of diapause eggs in summer can be high after rainfall (Ridsdill-Smith, 1997) and that there is a sharp decline in the development of post-diapause eggs at mean day temperatures above 20.5 °C (Wallace, 1970). Consequently, Farrow et al. (1993) made the prediction that regions that see an increase in summer rainfall would become less favourable for this pest. In addition, if pasture growth within a year and mite population growth become less synchronised we may experience less widespread outbreaks of this pest, assuming the mites do not rapidly adapt to the changing seasons.

The CLIMEX model (Hill, 2012) replicated the current distribution of this mite pest throughout southern and Western Australia well, but the baseline projection indicates that suitable conditions for this species can be found in northern New South Wales, where it has not been documented (Fig. 3). This is mostly due to the model not capturing stress to diapausing eggs over the summer due to high rainfall which will limit population persistence in this area. Regardless, the model shows that as the climate warms much of the area that is currently suitable for growth and development of *H. destructor* becomes less suitable in terms of a reduction in El values in certain regions across time (Fig. 3). Areas in southern Victoria, and especially Tasmania will experience more ideal conditions for this pest and may see an increased incidence of outbreaks; however conditions in Western Australia are less suitable by 2090.

2.2.1.4. Bird-cherry oat aphid, Rhopalosiphum padi. Rhopalosiphum padi L. (Hempitera: Aphididae) is a pest of cereals around the world. It is a highly mobile species (Parry, 2013) that causes direct damage from feeding, but perhaps is best known for the range of cereal viruses it transmits during the cooler autumn and winter months (Finlay and Luck, 2011; Parry et al., 2012; Valenzuela and Hoffmann, 2015). Rhopalosiphum padi reproduces sexually and alternates between grasses and cereal hosts, and in winter, cherry trees at different stages of its life-cycle (Table 2). In Australia, where both the environmental triggers for diapause and the obligate winter host plant are rare, the aphid reproduces asexually (Macfadyen and Kriticos, 2012). The CLIMEX model (Macfadyen and Kriticos, 2012) suggests that overall there is likely to be a

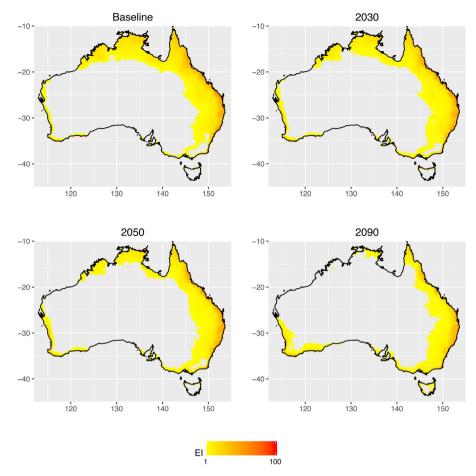


Fig. 2. The change in the suitable conditions for year-round growth of *Helicoverpa armigera* across Australia in response to climate change using a CLIMEX model for this species. Each model projection is shown as the Ecoclimatic Index (EI) ranging from 1 to 100. One scenario (A2) is shown and the consensus areas as an average between two Global Climate Models (CSIRO Mk3.0 and the Miroc-H) for the time periods 2030, 2050 and 2090.

decrease in the area suitable for year-round growth of *R. padi* by 2090 (Fig. 4). When we examine the spatial patterns of where this change in incidence is likely to occur we can see that Tasmania may experience increased pest presence from *R. padi* (Fig. 4).

2.2.2. Summary of case studies

For the four pest species that we examined in Australia (Table 2), general trends of poleward movement were projected, with pests tracking suitable environmental conditions and increased frequency in the southern parts of the projected distributions (Fig. 1). As suitable conditions for these pests move south, these regions may experience more outbreaks. Those species requiring cold conditions in order to break diapause and continue development are most likely to have their life-cycles disrupted. The outcome depends on whether the species has the physiological potential to continue its life-cycle across the whole year without entering diapause.

The models suggest that increased maximum temperatures in combination with reduced precipitation, and therefore an increase in desiccation potential, will make conditions less favorable for some current pest species in certain regions. However, there are limitations to the conclusions that can be drawn from the modelling approach used here. We cannot say what impact the interaction between abiotic factors such as temperature and wind speed may have on pests (e.g. Barton, 2014). Further development of climate change projections for pest species that include information on change in abundance within and between seasons would improve our ability to explain what these changes in risk

mean for pest damage to crops and ultimately yield loss. Whilst the change in incidence and damage potential may be small for some species, the economic consequences of this change could potentially be very large. Finally, the ability of these species to adapt to changing seasonality and host plant availability, in the wake of climate change, needs to be considered as we build on the capability of the models, thus we discuss implications of these in detail next.

2.3. Altering phenology

Overall increases in temperature will lead to faster development times and increased voltinism for many pest species (Table 1; Altermatt, 2010; Ziter et al., 2012), and may mean species become active earlier in the season (Harrington et al., 2007). Ouyang et al. (2016) used long-term data (since 1975) on Helicoverpa armigera (cotton bollworm) to explore the temporal trends in the species' dynamics. They found a shift to earlier eclosion of diapausing pupae due to increased temperature and an increase in the duration and abundance of adults in the overwintering generation. This led to more larvae recruited in the first generation, and greater damage to wheat crops early in the season. Earlier arrival of the potato leafhopper, Empoasca fabae across the United States has been correlated with warmer seasons (Baker et al., 2015). Furthermore, increased temperature further intensified the severity of infestations in alfalfa fields. These reported alterations in phenology may lead to asynchrony between pests and their natural enemies and could lead to release of some pests from

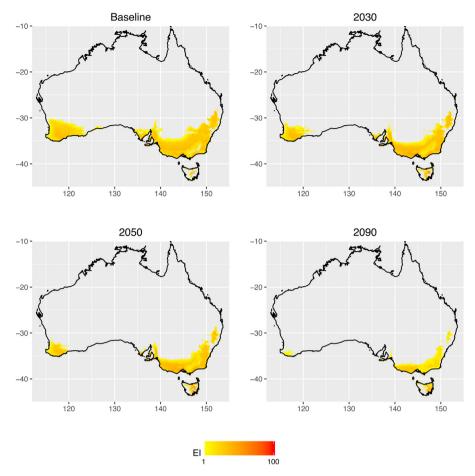


Fig. 3. The change in the suitable conditions for year-round growth of *Halotydeus destructor* across Australia in response to climate change using a CLIMEX model for this species. Each model projection is shown as the Ecoclimatic Index (EI) ranging from 1 to 100. One scenario (A2) is shown and the consensus areas as an average between two Global Climate Models (CSIRO Mk3.0 and the Miroc-H) for the time periods 2030, 2050 and 2090.

control. In contrast, Perez-Rodriguez et al. (2015) found synchronicity between summer migration patterns of aphids and their parasitoids within seasons in Europe, despite the timing of the first flight of aphids in spring steadily shifting forward. The models used in the case studies from Australia above have used phenological information to some degree and though not considered here, it is possible to use these models to examine how climate change may drive changes in population dynamics and voltinism (also see Li et al., 2015 for a model that explicitly incorporates phenology).

2.4. Phenotypic plasticity or evolutionary adaptation

The capacity of a species to adapt to changing conditions is an important characteristic that may lead to some species becoming pestiferous, or to further increase their impacts. Pest species may adapt to changes in climate either through phenotypic plasticity or genetic adaptation (Harmon et al., 2009; Hoffmann and Sgro, 2011; Catullo et al., 2015; Sgro et al., 2016). Being able to predict the likelihood and direction of such adaptive shifts and incorporate these into models is challenging. As climate change requires us to project changes in time, biological invasions which are "natural experiments" in space may form a useful surrogate to investigate the types of responses possible from pest species. Table 1 lists some examples of a pest's adaptation to changes in conditions following its introduction into a new geographic region. For example, the redlegged earth mite, Halotydeus destructor (see case study above) was introduced from South Africa in around 1908 and has since spread widely (Hill et al., 2012). Halotydeus destructor's historical distributional limits were linked to both temperature and moisture (Wallace, 1970). Recent modelling suggest that it has expanded its range into drier and hotter inland regions, beyond what was expected from conditions in the native range alone (Hill et al., 2012). In addition, laboratory experiments demonstrated that Australian populations had increased the upper thermal threshold for movement and were able to recover from cold stress more rapidly their South African counterparts (Hill et al., 2013).

There is an additional challenge in accounting for population level variability in response to environmental conditions. Currently, models typically assume homogeneity across populations and do not incorporate genetic diversity, connectedness and other processes such as founder effects. These processes are important when considering how adaptations are propagated between populations. Adaptive shifts are not often incorporated into climate change models, and so the relative importance of these in assessing climate change impacts is largely unknown (Coope, 1993).

3. Indirect effects of a changing climate on pests

Indirect impacts of climate change on pests are those that are mediated by bottom-up processes associated with host plant resources, or top-down processes associated with natural enemies. Even simple indirect interactions can have significant consequences for crop losses. For example, frost is known to directly damage flowering wheat plants and therefore lead to reduced yield, but it may also increase wheat susceptibility to aphid pests (Lacoste

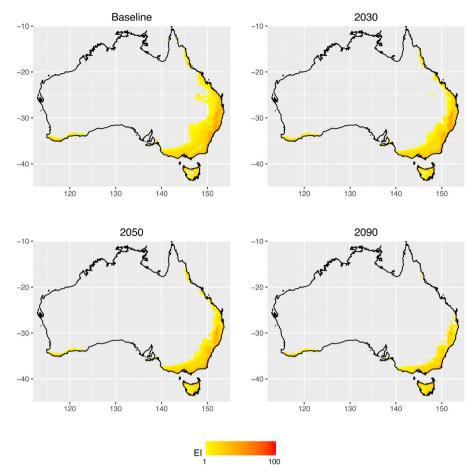


Fig. 4. The change in the suitable conditions for year-round growth of *Rhopalosiphum padi* across Australia in response to climate change using a CLIMEX model for this species. Each model projection is shown as the Ecoclimatic Index (EI) ranging from 1 to 100. One scenario (A2) is shown and the consensus areas as an average between two Global Climate Models (CSIRO Mk3.0 and the Miroc-H) for the time periods 2030, 2050 and 2090.

et al., 2015). Often indirect impacts are more difficult to quantify but they are starting to be incorporated into impact studies.

3.1. Natural enemies

Current levels of pest control services supplied by natural enemies (predators and parasitoids) vary considerably across time, but like pests these species abundances and behaviors can be related to temperature and precipitation patterns (Thomson et al., 2010). In general it is assumed that species at higher trophic levels are more vulnerable to the effects of changing climate (Jeffs and Lewis, 2013). Thermal performance curves of natural enemies generally have lower tolerance to high temperatures in comparison to their prey's thermal tolerance curves (Montserrat et al., 2013). However, this effect can be alleviated or exacerbated by interactions with other factors. Dosdall et al. (2012) showed that high temperatures and certain brassica host plant species differentially affected the development of the parasitoid, Diadegma semiclausum, compared to its host, the pest diamondback moth (Plutella xylostella). Furthermore, significant differences have been found between constant and fluctuating temperature regimes for development parameters in laboratory studies involving diamondback moth, and its North American parasitoid, Diadegma insulare (Bahar et al., 2012). In a separate study Romo and Tylianakis, (2013) found that elevated temperature and drought effects interacted to reduce the effectiveness of parasitoids of cabbage aphids. In contrast, a modeling study demonstrated that biological control of aphids by ladybeetle predators was strengthened under increasing temperatures in the model (Abbott et al., 2014). This was due to greater predation rates and shorter handling times for predators at higher temperatures.

3.2. Community-level impacts

Whilst there are a growing number of examples of laboratory experiments investigating the impact of changes in temperature or carbon dioxide on plant-pest-natural enemy interactions (e.g. Reddy et al., 2004; Yin et al., 2009), it can be challenging using these studies to draw conclusions at the whole-community-level. More complex experimental arenas, that include multiple species, offer the opportunity to study both direct and indirect effects across multiple trophic levels. For example, Dong et al. (2013) used infrared warming devices in a wheat field in northern China to examine the effects of warming and tillage on interactions between wheat plants, aphids and parasitoids. Temperatureinduced acceleration of winter wheat phenology resulted in increased aphid abundance (mean number of aphids in warmed plots was 57% higher than that in control plots), but the response of parasitoids to warming varied according to their yearly population fluctuations. Similarly, long-term historical data sets on natural enemies and patterns of pest control services, from which inferences about climate drivers can be made, are rare. A metaanalysis of 15 lepidopteran larvae-parasitoid interaction data sets showed a decrease in parasitism levels as climatic variability increased (Stireman et al., 2005). This suggests we may see an increased frequency of pest outbreaks through a disruption of herbivore-parasitoid dynamics in response to greater climate variability. Two historical data sets (1921–1928, and 2001–2005) on larval parasitoid communities of *Ostrinia nubilalis* (maize pest the European corn borer), and sister species *O. scapulalis* have been used to assess long-term changes in parasitoid communities (Folcher et al., 2011). Over this time period there was a substantial decrease in parasitism rate of *O. nubilalis* but no reduction in species richness of the parasitoid community (although there was species turnover). In contrast, *O. scapulalis* had a decline in species richness, but no decline in parasitism rate (Folcher et al., 2011). Such species interactions can alter species responses to climate change and future work needs to focus on including this complexity in experimental studies (Gilman et al., 2010).

Indirect impacts of climate change can propagate throughout a community of connected species in an ecosystem, however few studies have quantified these impacts. For example, Barton and Ives (2014) found in a field experiment that spotted aphid densities were three times higher on alfalfa plants under a drought treatment compared to an ambient treatments with high pea aphid densities. This was due to an indirect effect of the drought treatment on the spotted aphids. Water stressed alfalfa plants had lower population growth of pea aphids, and therefore were less attractive to the generalist ladybeetle predator. The spotted aphids also suffered less predation in the drought treatments and could therefore reach high abundance. We know that the incorporation of species interactions into models can alter species responses to climate change and future work needs to include this complexity in experimental studies (Gilman et al., 2010).

3.3. Changes in management practices

In addition to the impact of climate change on pests, there are indirect changes driven by changes to agricultural practices that may impact pest outbreak potential (Ewald et al., 2015). For example, there has been a widespread adoption of minimumtillage or no-till across southern grain production regions in Australia, mainly to improve water conservation and prevent soil erosion that is exacerbated during dry years. However, this practice is associated with an increase in slug, snail, false wireworm, cockchafer and other detritivore-turned pest problems due to the creation of more favorable habitats for these invertebrates (Hoffmann et al., 2008). There has also been a recent shift to using canola as a break crop in rotation with wheat, which is more susceptible to damage from emergence pests such as earth mites and lepidopteran pests such as P. xylostella (Gu et al., 2007; Furlong et al., 2008). This makes it challenging to elucidate whether an increased frequency of pest outbreaks in a region is due solely to climate change.

4. Facilitating adaptation to climate change in a farming system context

Variability in seasonal conditions has long driven changes in farming practices as has the development of new tools and crop varieties to optimise yield (Olmstead and Rhode, 2011). For example, decreased frost frequency and the availability of new wheat varieties have allowed wheat crops in central Queensland, Australia, to be planted 3–4 weeks earlier (Howden et al., 2010). In this context, adaptation can be defined as adjustments to farming systems in order to moderate the pest risk associated with likely changes. There are a number of pest management options that could be recommended (Table 3) based on the change in potential projected from models and other information sources we have outlined here. Importantly, many "fail-safe" management options are currently available that do not require models with greater

accuracy or precision to be developed. Some management options may simply represent a move towards more sustainable pest management (Lobell, 2014), and may be beneficial for other threats not related to climate change. Finally, some management options are difficult to implement because they require many changes to farm business decisions and may have up-front costs (Table 3). The change in pest damage potential must be high to warrant farmers engaging in these management options.

Adaptive management strategies for pests are ongoing processes that require dynamic decision-making in response to observed changes, and will therefore need to be integrated into adaptation strategies targeting crop productivity under climate change. An example of where such an adaptive strategy for pests has been used successfully is in the management of resistance in Helicoverpa species in Australia's GM cotton systems (Downes et al., 2010). In this example, monitoring the frequency of resistance alleles in pest populations allows for a better informed mitigation strategy for resistance management in cotton, and an early warning system for failures of the GM technology (Downes et al., 2010). There are also so-called maladaptive management tactics; these are generally short term in focus and reduce flexibility and stifle problem-solving by farmers (Allison and Hobbs, 2004). A prevalent example is the prophylactic application of inexpensive, broad-spectrum insecticides. This tactic is employed to reduce the likelihood of immediate crop loss, especially if the pest levels are high and continuous, but it is also used to save time for growers and their advisers, especially when monitoring is perceived to be too time-consuming and expensive. As pest potential reduces overall, or becomes more variable from season to season, the benefits of this approach are increasingly outweighed by the risks of resistance, non-target impacts, and secondary pest outbreaks. In any case, this approach reduces natural enemy populations and masks the underlying population cycles of pests. Under such circumstances, farmers cannot learn from observing the natural cycles that would enable them to adjust their approach in future seasons, resulting in a treadmill of continued reliance on insecticides.

5. Critical knowledge gaps

Further development of tools required for adaptive management of pests today will increase the likelihood of a successful climate change adaptation strategy. The inherent challenge is identifying aspects of management that can benefit from currently available tools, and then using the gaps to suggest new directions for research, development and tool construction. The four areas we have identified as critical are:

5.1. Models of pest outbreak potential

Species distribution models are useful for making projections about large-scale changes to species range under future climate change scenarios, as with the case studies above, but are less useful for estimating if and when pests will reach high abundances in a season. Simulation models focused on population dynamics and critical events in pest life-cycles are better suited assessing the likelihood of pest outbreaks (McDonald et al., 2015). One of the challenges of this approach is the availability and accuracy of downscaled climate projection data. Models that include agronomic factors that increase or decrease outbreak potential are also useful for assessing the impacts of management changes that may minimize pest risk prior to the season starting. Such models are important for improved pest management decision-making under today's climate, and will provide added benefits under more variable climate conditions.

5.2. Incorporation of pest impacts into global crop models

Incorporation of biotic stressors such as pests, weeds and disease into global crop models that examine the potential impacts of climate change on crop productivity needs to become a priority (Gregory et al., 2009). Whilst it is unrealistic to think this can be achieved for all grain pests, incorporation of few of the more widespread and economically damaging species is feasible. The development of a modular approach to biotic stressors, where submodels for different pests can be included or excluded from crop models, will allow us to say when and where these biotic stressors will limit crop productivity under future climates. Importantly, we have a number of management options available for limiting losses from biotic stressors that will be equally useful under future climates that can be implemented in response to increased pest potential (Table 3). The incorporation of temporal pest dynamics into crop models will be especially useful for understanding shifts in synchrony between the timing of crop growth and the likelihood of pest damage (e.g. Lee et al., 2016). Again, there are multiple management options (e.g. different planting windows, different cultivars that mature at different rates, Table 3) that can be implemented to address increased risk.

5.3. Monitoring of existing pests and surveillance for new pests

Currently, long-term monitoring strategies to track changes in pest abundance or distribution in grain production landscapes are limited to a few countries (e.g. the EXAMINE network of suction traps and light-traps in Europe) (Harrington et al., 2004). There is some *ad hoc* recording of pest outbreaks, and some piecemeal records of pesticide inputs but this data is not often consistent across countries and certainly not within Australia. The development and automation of monitoring technologies and metrics, and the maintenance of open access databases of pest incidence that can track changes in the frequency or severity of pest outbreaks, are required to develop an effective climate adaptation strategy. Such systems are also needed to feedback data about observed broad-scale changes to farmers. Further research around what indicators we need to measure, and the most cost effective way to collect and warehouse this data, is a necessary first step.

5.4. Impacts on natural enemies—generalizations to help decision-making

The impact of climate change on natural enemies and its subsequent effect on pest control services are not well understood (Jeffs and Lewis, 2013; Eigenbrode et al., 2015). Currently research is focused on exploring all the idiosyncratic differences between species that may lead to different responses. However, studying every specific species interaction is impractical: it is an enormous undertaking and may generate findings applicable only to a limited area. Farmers need options that can be implemented now if they are to have any hope of offsetting some of the negative changes that are occurring. A greater focus on finding commonalities across species and communities in their response to changing climate is needed. This involves two processes: firstly, bringing together the information we currently have on specific-species interactions and using these to assess how climate change impacts the broad ecological processes that underlie these interactions (Crowder and Harwood, 2014). Secondly, assessing climate change impacts at the community-level and identifying how climate change impacts different functional groups and traits. Conceptual models are already available to aid in this process (Schmitz and Barton, 2014). Both these approaches will allow general principles to be incorporated into management options, even in regions with relatively little information on natural enemy ecology (i.e. a more generalized approach to understanding climate change impacts). Furthermore, they will highlight species interactions for which we have little information but for which detailed studies could alter the adaptation options suitable for farmers.

6. Conclusions

Some of the projections about the likely impact of climate change on crop yield broadly suggest a reduction in productivity and more variability from season to season (Luo and Kathuria, 2012; Zheng et al., 2012). Nonetheless, we have illustrated through four case studies that there are potential 'winners and losers' and that there are multiple management options available for addressing a range of potential outcomes. However, some options that may have worked well in the past (e.g. heavy reliance on inexpensive pesticides, widespread use of a few crop types a few varieties and synchronized agronomic practices) are maladaptive and likely to be less successful in the future. A greater emphasis on understanding likely impacts on individual pest species but within the context of impacts at the community-level is required. We identify here some critical knowledge gaps, in particular knowledge of the indirect impacts of climate change on pest species' distributions and outbreaks, such as top-down impacts on natural enemies and bottom-up feedbacks between pests and their plant hosts. Incorporating more sustainable management practices in the short-term will help improve pest management under climate change. Building on this increased understanding, we need tools to support adaptive management under future climates including simulation models of pest outbreaks, incorporation of pests into global crop models, monitoring for existing pests linked to surveillance for new pests, and generalizations around impacts on natural enemies to help with pest management decisionmaking.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.08.029.

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