2 Species Distribution Modelling in Predicting Response to Climate Change

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Abstract

Species distribution modelling comprises a range of widely used tools for predicting potential changes in insect pest species distributions with climate change. We review the current literature to see the effectiveness of different approaches, particularly in comparing predictions based on current distribution data (correlative or 'environmental niche models') and those based on life-history traits and determination of thermal limits (mechanistic models). We review new developments in implementing processes such as dispersal and biotic interactions within species distribution models and how these could be used to develop management strategies incorporating natural enemies into climate change predictions. We propose that species distribution models should be linked with key trait data where possible to inform better of response to climate change.

2.1 Introduction

Many species of invertebrates not only cause huge losses to biodiversity through competition and disruption to ecosystem function (Ostberg *et al.*, 2013; Zhou *et al.*, 2013), but also represent some of the most recognized causes of agricultural crop loss through both herbivory and competition, and as vectors of disease (Ziska *et al.*, 2010). Further to this, there are many invertebrate species that pose serious concerns for human health, particularly mosquito vectors (Bai *et al.*, 2013; Lee *et al.*, 2013) and ticks (Morin and Comrie, 2013; Porretta *et al.*, 2013). Climate change will result in a range of potential impacts on pest invertebrates (reviewed in Harrington and Woiwood, 1995), including changes in population dynamics such as growth rate and overwintering success, as well as an increase in the number of generations per year and changing interactions with other species (Van der Putten *et al.*, 2010; Sutherst *et al.*, 2011). Greater risks are likely to come from changes in geographic distributions of pests and invasions by new pests (Harrington and Woiwood, 1995). For example, the distribution shifts and greater outbreak potential of the coffee borer beetle, *Hypothenemus hampei* Ferrari, in Africa (Jaramillo *et al.*, 2009), and the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in North America (both Coleoptera: Curculionidae) (see de la Giroday *et al.*, 2012), and the pine processionary moth, *Thaumetopoea pityocampa* Schiff (Lepidoptera:

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Thaumetopoeidae), in Europe (Battisti *et al.*, 2005), are all linked to climate change.

Pest invertebrate species cause extensive damage to a wide range of economically important industries such as fruit and horticulture, pasture and broadacre crops including oilseeds, cereals and pulses. While drivers such as changes in pesticide use and increased irrigation are likely to be associated with some shifts in species distributions, climate change is likely to be driving shifts in the geographic distribution of some pest invertebrate species (Hoffmann *et al.*, 2008). With changes in distribution come changes to phenology and persistence that ultimately lead to pest outbreaks and spread of vector-borne plant pathogens. Some species, such as armyworm (Lepidoptera: Noctuidae), may be responding negatively to climate change (Hoffmann *et al.*, 2008). Others, such as the slug, *Milax gagates*, which perform better in arid conditions, may benefit from drier conditions under climate change (Nash, 2008; Domisch *et al.*, 2011; Jiang *et al.*, 2013), and so too the transmission of plant viruses, such as Yellow dwarf by aphid vectors (Parry *et al.*, 2012). Clearly, pest species will respond to climate change differently, and it is thus important to investigate individual species' responses through a framework that is broadly applicable.

To meet the challenges that climate change will impose on food production, we need to be able to predict accurately how pest species will respond. To date, research on how invertebrate pests will respond to climate change is relatively rare (Mika *et al.*, 2008; Ziter *et al.*, 2012). Such research could help in the development of management recommendations to be used by growers to aid crop protection in the future (Steffen *et al.*, 2011; Turner *et al.*, 2011). For this to be achieved, a good understanding is required of how species have adapted in the past, how they respond to current variability in weather, and when and how this is likely to lead to pest outbreaks across agricultural landscapes. An essential component of this is to predict species distributions across the landscape.

2.1.1 Predicting distributions of pest insects

The link between insects and climate was researched widely even before the field of ecology was formally recognized. When Uvarov (1931) reviewed this subject, he cited over 1000 papers, many of which dated back to the 19th century or earlier. At this time, the field of 'climatic analysis of insect distribution' was first formulated. Meteorological data were available to ecologists and the understanding of how large-scale climatic variables influenced distributions was becoming apparent (e.g. Grinnell, 1917). While there existed a few studies that studied the effect of climatic variables on pest insects: for example, alfalfa weevil (Ball, 1917), green bug, *Schizaphis graminum* Rond. (Ruggles and Wadley, 1927), and Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Gjullin, 1931), it was William C. Cook who outlined methods of predicting the distributions of pest invertebrate species (Cook, 1931). Within these methods, Cook (1929) described how weather station data could be used initially to determine climatic zonations for pest insects. He explained how these zones could be correlated with the frequency of limiting climatic conditions and thus provide maps describing where outbreaks of species such as the pale western cutworm, *Porosagrotis orthogonia* Morr. (Cook, 1924), and the true armyworm, *Cirphis unipuncta* (now *Mythimna unipuncta* (Haworth)) (Cook, 1929), were more likely to occur. Cook went on to describe a framework for predicting insect distributions that tied weather data to insect distributions and known physiological parameters (Cook, 1931). While the effects of 20th century climate change were not apparent at this time, and the field of invasion biology was just emerging, this provided a robust framework for predicting the distributions of pest invertebrates in relation to climate. (For another account of Cook's contribution to the field of predicting pest insect distributions in relation to climate, a recent paper by Sutherst (2014) gives further detail.)

There have been many other advances in the field of pest ecology and distributions since the time of Cook (e.g. Messenger, 1959; Andrewartha and Birch, 1982), but predicting the distribution of a pest species still remains an essential component of understanding the potential effects of climate change. Today, we are faced with enormous challenges posed by a changing climate and increasing introductions of insect pests through global trade and tourism, and we require tools, methods and competent practitioners to meet them.

In this chapter, where we review the prediction of pest invertebrate response to climate change through the use of modern tools, it is still useful to consider the ideas of Cook (1931). Central to predicting potential distributions for pest insect species and response to climate change is the concept of the *niche*.

2.2 Niche Concept

2.2.1 Niche definitions

The niche is an ecological concept that ties biotic and environmental elements together (Keller and Golley, 2000) to define the distribution or functional role of a species. To describe the niche for a given species accurately would involve measuring every environmental condition, biotic interaction and resource that an organism requires (Porter and Kearney, 2009). In reality, this is an impossible task; however, the niche as a concept still serves as a useful tool for understanding species' requirements across space and time (Soberón and Nakamura, 2009; Wiens *et al.*, 2009). In terms of predicting the distribution of species, there are different and equally important interpretations of the niche that need to be defined when investigating processes and traits that determine niche boundaries (Colwell and Rangel, 2009; Porter and Kearney, 2009; Wiens *et al.*, 2009).

The first formal definition of the niche was provided by Joseph Grinnell, who described the niche in terms of areas of distributions of species and the different variables that govern the range of species (Grinnell, 1914, 1917). That is to say, that the spatial extent of the range and geographical expression of a species' niche are approximately the same (Tingley *et al.*, 2009). This provides a somewhat restricted definition of the niche, employing broad, non-interacting ecological variables (Soberón and Nakamura, 2009) to set the range limits of species (Wiens, 2011). This simplicity allows for an operational and straightforward niche concept (Soberón and Nakamura, 2009) and, when employed, can provide strong explanations of species' range boundaries (Tingley *et al.*, 2009). Such an interpretation of the niche lends itself to being particularly useful in understanding biogeographical patterns (Wiens, 2011).

While the Grinnellian niche encapsulates broad environmental processes, Charles Elton defined the niche in terms of biotic interactions and resource limitations that shaped the distribution of a species (Elton, 1927; expanded by Soberón, 2007). This interpretation of the niche presents the species as playing a functional role within a community (Wiens *et al.*, 2009), and is thus a much finer-scale concept than that of Grinnell. The Eltonian niche employed axes of resource utilization and provided the foundation for later elaborations by Hutchinson (1957) and MacArthur (1972), to become widely used in ecological studies (Wiens *et al.*, 2009). This interpretation of the niche allows for understanding of the biophysical requirements of the species to be measured and associated with landscape features, to define niche boundaries.

In later development of the niche concept, George Evelyn Hutchinson (1957) presented a niche–distribution duality that provided perhaps the most important distinction of niche concepts termed fundamental and realized niches. Hutchinson described the niche as taking both the form of the *fundamental* niche – the direct physiological requirements of a species – and the *realized* niche – the proportion of the fundamental niche actually occupied by the species at a particular time, due to limits set by both biotic and abiotic interactions (Wiens

et al., 2009). This Hutchinsonian definition of the niche allows for both the Grinnellian and Eltonian niche interpretations to be employed in a suite of species–environment relationships within physical (environmental) and geographical (biotope) space (Colwell and Rangel, 2009; Wiens *et al.*, 2009).

The growth of species distribution model use has seen the advent of the *potential* niche. This describes the area that might permit population persistence and growth, but to which the species has not yet dispersed (Soberón, 2007; Soberón and Nakamura, 2009). This concept is particularly important for pest and other invasive species that are not in equilibrium with the environment.

2.2.2 Niche conservatism

When measuring the response of pest insects to climate change, it is important to understand how the species–environment relationships are likely to persist or change. A species that occupies geographical regions corresponding to regions of niche space set by the fundamental niche is said to have displayed niche conservatism (Colwell and Rangel, 2009). Conversely, niche 'shifts' describe transgression between species–environment relationships across ranges (e.g. Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007) or over time (e.g. Kharouba *et al.*, 2009). For studies of climate change, niche conservatism refers to species that track climatic change to preserve species–environment relationships: species must undergo elevational and/or latitudinal range shifts to stay within their favourable climate zones (Colwell and Rangel, 2009). This process can cause problems for species not able to disperse as fast or as far as the changing climate dictates.

Niche shifts may occur if the native range holds only a subset of the full range of the fundamental niche due to interspecific competition (the presence of predators and pathogens), or a geographical barrier, or a limited set of possible environments – the species in its invasive range might simply be

expressing other parts of the fundamental niche (Broennimann *et al.*, 2007; Rödder and Lötters, 2009; Alexander and Edwards, 2010; Medley, 2010). Alternatively, the species may have adapted, resulting in a change in a species' response to environmental variables over time (Broennimann *et al.*, 2007; Ficetola *et al.*, 2010). A niche shift may also arise through species dispersal and colonization, driving expansion geographically into new environmental habitats (Alexander and Edwards, 2010). These processes of range expansion may be facilitated by changes in climatic conditions, land use or through evolutionary adaptation.

Measuring niche conservatism can give insight into predicted pest insect response to processes such as climate change and biological invasion, including the interaction of these two. In this chapter about modelling insect pests and climate change, we describe tools to measure niche conservatism geographically and look at examples from both biological invasions and climate change research, as these fields are highly relevant to one another. One way in which we can study the process of niche shifts and niche conservatism in response to climate change is to construct different types of species distribution models. These models can be used to inform which environmental variables and traits may limit the niche, and the level of niche conservatism displayed in species invasion and response to climate change.

2.3 Species Distribution Models

Species distribution models are increasingly popular tools for describing the niche of a species and detecting niche shifts. There are a number of modelling methods available that have varying advantages and explicabilities, and which utilize different interpretations of the species niche. Commonly used in conservation biology research (Pearson *et al.*, 2007; Habel *et al.*, 2011), species distribution models may also be applied to invertebrate pest species, especially when questions need to be asked of species invasion or climate change impacts. Importantly,

the choice of which type of model to use relies heavily on the type of data you have available. It is also crucial that as much information about the species as possible is included to ground some of the choices during the modelling process.

Table 2.1 gives examples of recent research showing the application of species distribution models for a variety of pest insects. At present, the majority of pest insect distribution models determine potential areas for species invasions, though more are starting to address responses to climate change.

Much of the recent advance in species distribution modelling has been made possible by the increasing availability of global weather station data and the computational power to process these. This has allowed for the formation of geospatial databases that offer high-resolution layers of averaged monthly climate data (e.g. WorldClim (Hijmans *et al.*, 2005), ANUCLIM (v6.1, Fenner School of Environment and Society, Australian National University)). These data can be transformed into biologically relevant trends and patterns of rainfall, temperature, humidity and solar radiation (e.g. BIOCLIM variables (Nix and Busby, 1986)), and used to determine limiting factors to species distributions (Elith and Leathwick, 2009). Instead of models being restricted to a few sites, it is possible to project models across entire countries, continents or globally, to understand the macroecological processes of invasion and climate change (Peterson, 2003; Araújo *et al.*, 2005; Elith and Leathwick, 2009). There is also a range of future climate models (global circulation models – GCMs) that are based on different scenarios of the severity of climate change. These allow for future forecasts of climate change to be incorporated into species distribution models. Choice of climate change scenario can alter model outputs, so this needs to be taken into consideration when building models, to determine which scenarios are likely to be relevant to the models (Beaumont *et al.*, 2008; Mika and Newman, 2010). As no one model may be considered the 'best' (Beaumont *et al.*, 2008), an ensemble forecast of a range of GCMs can outperform single GCMs and provide greater confidence in model outputs (Fordham *et al.*, 2011).

While the toolbox is increasing for species distribution modelling, there is little chance that automation will ever take hold (see Sutherst, 2014), and generalizations are likely to be only for large-scale studies rather than for effective management at the landscape level (e.g. general poleward movements; Bebber *et al.*, 2013). Selection of the most appropriate model requires careful consideration of the species and the data available for the species, which will be different in terms of forms and amount. There is no 'one size fits all' approach for modelling pest insect species, and this needs to be taken into consideration. The range of models presently available are suited to different tasks and use types of data in different ways, and it may often be that applying different types of models to the same species, allowing for determining congruence between predictions, is a better approach (Venette *et al.*, 2010).

There is a wealth of literature on the application of different species distribution models, and there are many debates surrounding the application and validation of such models. Here, we present a brief overview of the currently popular methods of species distribution models being applied to questions surrounding pest insects and climate change; ecological niche models, mechanistic models and a semi-mechanistic approach, CLIMEX (see Fig. 2.1).

2.3.1 Ecological niche models

Species distribution models that attempt to characterize the niche by correlating known distribution points with environmental predictor variables, or covariates, are typically referred to as ecological niche models (ENMs) (Jiménez-Valverde *et al.*, 2011; Wiens, 2011). ENMS investigate something close to the realized or potential niche of a species by correlating limiting variables identified from the landscape the species is found in to suitable habitat in appropriate geographic areas (see Elith

Table 2.1. Examples of species distribution models for pest invertebrate species.

Common name	Species	Models	Type	Use	Locality	Reference
Fig fly	*Zaprionus indianus*	MAXENT/GARP/ Mahalanobis distances	Correlative	I	Global	da Mata *et al.*, 2010
Western corn rootworm	*Diabrotica virgifera virgifera*	ENFA/Mahalanobis distances	Correlative	I/C	Northern hemisphere	Aragón and Lobo, 2012
Yellow-legged hornet	*Vespa velutina nigrithorax*	Ensemble modelling	Correlative	I/C	Global/Europe	Barbet-Massin *et al.*, 2013
Mediterranean fruit fly/ Natal fruit fly	*Ceratitis capitata/Ceratitis rosa*	GARP/PCA	Correlative	I	Africa/Europe/global	De Meyer *et al.*, 2008
Asian tiger mosquito	*Aedes albopictus*	CLIMEX/MAXENT	Semi-mechanistic/ correlative	I/C	Australia/global	Hill *et al.*, 2014
European grapevine moth	*Lobesia botrana*	Physiology/demographic	Mechanistic	I	California/USA	Gutierrez *et al.*, 2012
Light brown apple moth	*Epiphyas postvittana*	Temperature/demographic	Mechanistic	I	California	Gutierrez *et al.*, 2010
Light brown apple moth	*Epiphyas postvittana*	CLIMEX/MAXENT	Semi-mechanistic/ correlative	I	Global	Lozier and Mills, 2011
Bird cherry-oat aphid	*Rhopalosiphum padi*	CLIMEX	Semi-mechanistic	I	Global	Macfadyen and Kriticos, 2012
Pea leafminer	*Liriomyza huidobrensis*	CLIMEX	Semi-mechanistic	I/C	North America	Mika and Newman, 2010
Swede midge	*Contarinia nasturtii*	CLIMEX	Semi-mechanistic	I/C	North America	Mika *et al.*, 2008
Spruce budworm	*Choristoneura fumiferana*	Ecophysiology/temperature	Mechanistic	C	North America	Régnière *et al.*, 2012
Brown marmorated stink bug	*Halyomorpha halys*	MAXENT	Correlative	I	North America/global	Zhu *et al.*, 2012

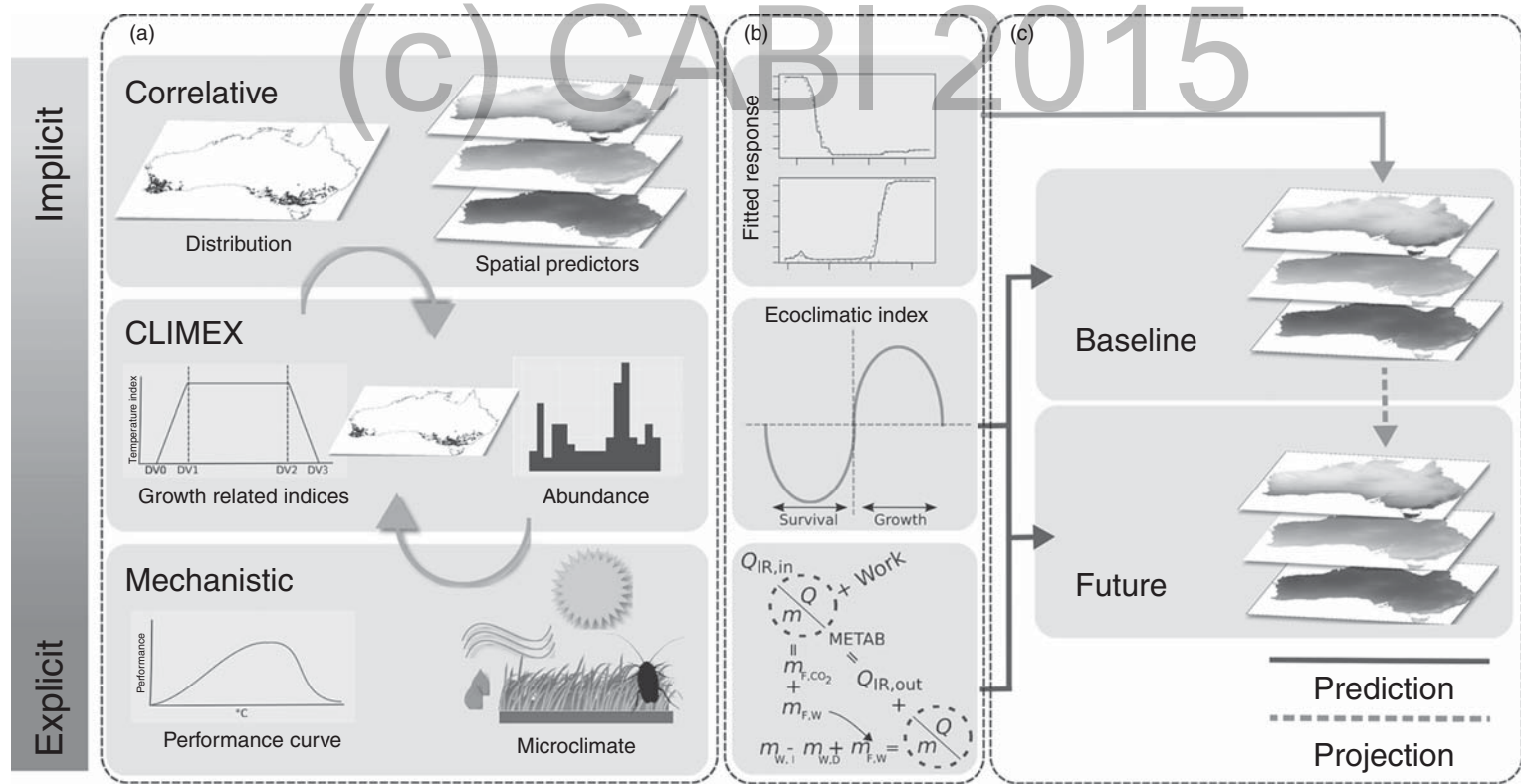*Note:* I = invasion risks; C = response to climate change.

(a)

Implicit

Correlative

Distribution

Spatial predictors

CLIMEX

Temperature index

DV0 DV1 DV2 DV3

Growth related indices

Abundance

Explicit

Mechanistic

Performance

°C

Performance curve

Microclimate

(b)

Fitted response

Ecoclimatic index

Survival Growth

$Q_{IR,in}$ $+ Work$

Q

m METAB

$=$

m_{F,CO_2} $Q_{IR,out}$

$+$ $+$

$m_{F,W}$ Q

$m_{w,i} - m_{w,D} + m_{F,W} = m$

(c)

Baseline

Future

Prediction

—————

Projection

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Fig. 2.1. Schematic illustration showing general differences between types of species distribution models (SDMs) used in predicting the response of insect species to climate change. (a) Displays the different categories of SDM mentioned in this chapter and the data sets they incorporate. (b) Displays how those data are fitted in the model. (c) Displays how the fitted models are then either spatially predicted or projected to new climate surfaces. Explicit and implicit scale is adapted from the review in Kearney and Porter (2009). *Correlative models* (typically called *ecological niche models*) combine known localities of species (presence-only or presence-absence records) with spatial predictors at each of these locality points to model species–environment relationships. Fitted functions for response to incorporated variables are then combined to determine the species–environment relationships, and then this can be predicted to the spatial data the model was trained on, or projected (extrapolated) on to new spatial predictors, such as climate change scenarios.

et al., 2011 for a more detailed explanation). Using such models, it is possible to predict pest insect species range boundaries and project these models into future climate change scenarios (extrapolation) to investigate how changing climate space may influence broad-scale species–environment relationships.

There is an increasing variety of correlative methods available to predict the distribution of species, ranging from regression methods such as GLMs (generalized linear models) and GAMs (general additive models), bioclimatic methods such as BIOCLIM and ENFA (environmental niche factor analysis) and through to more recently developed machine-learning methods, MAXENT (maximum entropy) and BRTs (boosted regression trees). A prerequisite for using all these types of ENMs is having sufficient distribution data to characterize the species–environment relationships across the geographical ranges that are likely to determine the distribution. In turn, good distribution data provide a clear advantage of a robust model being built, with little knowledge of the species' ecology and biology required (although to present a model in isolation of this will provide little benefit). One of the key points of using distribution information is that these points are the result of many different ecological processes (Sutherst, 2014). That is, when applying correlative models, the data being included could represent any number of possibilities that translate into a presence point. Presence points do not always represent population persistence, and thus it is imperative to understand which data are useful to the modelling process.

Different forms of distribution data will again dictate which of these model types is most appropriate to the species question in hand, including amount of distribution points, the prevalence of those points across a given area and whether there is absence data as well as presence data. For instance, MAXENT and ENFA require presence-only data (with an ecologically defined background, or study area), whereas BRTs can employ presence and true (surveyed) absence data. What ENMs all have in common, however, is the requirement of well-sampled and unbiased data to construct models that encapsulate as broad a range of species–environment relationships as possible. Ideally, species–environment relationships in both the native and invasive ranges need to be characterized (Beaumont *et al.*, 2009; Jiménez-Valverde *et al.*, 2011). For many pest insect species, the only data available are for where a species has been found (e.g. outbreaks) or abundance data, thus the correlative models in Table 2.1 are all based on presence-only data. These data need to be checked closely for errors, and often require expert opinion to confirm the validity of distribution data. For more information on spatial biases and sampling errors and how they influence models, Dormann *et al.*

Fig. 2.1. *continued*

CLIMEX draws from different knowledge domains (e.g. physiological response, distribution data and abundance data) to determine an ecoclimatic index that is a combination of growth and stress indices (redrawn from Sutherst *et al.*, 2004). This is run across weekly values throughout a year and then combined into a yearly summary of population growth and survival seasons (adapted and redrawn from Sutherst, 2003). In this way, models can be run for a given locality or across gridded spatial predictors, to produce maps of geographic suitability based on the ecoclimatic index. By running the model on future climate scenarios, CLIMEX is able to avoid the inherent issues of extrapolation that correlative models incur.

Mechanistic models take physiological information measured on the species to define limits to distributions based on processes and ecophysiological profiles. While mechanistic or process-based models can take many forms, the stylised one here combines performance curves and information about the microclimate (adapted, with parts redrawn from Kearney and Porter, 2009). Models can be based on how the species experiences the environment, how this affects metabolic rate and what this ultimately means to distributions and phenology under both current (baseline) and future conditions. Additionally, mechanistic models may be able to incorporate biotic interactions as explicit processes to examine the effects of climate change on pest insects and competitors/predators (see text for more detail).

(2007) and Elith and Leathwick (2009) provide reviews.

Because biotic and abiotic factors, and dispersal constrain the niche, ENMs can provide only partial information on the full range of environmental conditions that the species may survive (i.e. not estimating the fundamental niche, or even the potential niche) (Jiménez-Valverde *et al.*, 2011). Related to this there are two main criticisms when using correlative models for measuring biological invasion and response to climate change.

The first of these criticisms is that environmental limits may be different between populations (particularly across both native and invasive ranges), inhibiting the ability of models to describe both ranges (Randin *et al.*, 2006). For instance, when characterizing the realized niche of the native range, the species may be inhibited by a range of barriers, including biotic and abiotic factors that do not exist in the invasive range (Beaumont *et al.*, 2009), resulting in underestimation of the potential invasive niche. Further, insect pest species are often not in a state of equilibrium with their environment, particularly within novel, invaded ranges (Václavík and Meentemeyer, 2009). This may translate into geographic range expansions as species continue to spread to fill their potential niche (Soberón, 2007; Soberón and Nakamura, 2009) and give rise to issues with ENM predictions. However, there are some techniques to help with these issues; see Elith *et al.* (2010) and Hill and Terblanche (2014) for examples of using presence-only data for range-expanding species. This non-equilibrium may be further exacerbated through climate change.

The second group of criticisms surrounds the use of ENMs as reliable tools for extrapolating into new space or time. Some degree of caution must be taken when projecting ENMs, as the relationship of variables projected may result in underprediction of areas that will contain non-analogue climates. Therefore, when ENMs are used to measure niche conservatism and response to climate change, they inherently encompass a broad range of factors and include the possibility that niche shifts are not a result of change in the fundamental niche (Hill *et al.*, 2012). A good primer on the application of the transferability of correlative species distribution models is found in Elith and Leathwick (2009).

In the absence of strong biotic interactions, as is often the case for pest insect species, it is possible to explore modelled responses and apply ENMs in an attempt to account for unstable relationships with climate, and as yet unencountered environmental conditions (e.g. Elith *et al.*, 2010) such as climate change. Given good distribution data in both native and invasive ranges (characterizing the realized niche as much as possible), correlative models have been demonstrated to be valuable tools for modelling pest insect distributions in relation to climate change.

2.3.2 Mechanistic models

Mechanistic models are often referred to as process-based (Morin and Thuiller, 2009) or trait-based (Kearney *et al.*, 2008) models and use explicit biological processes built on species-specific observations (Morin and Thuiller, 2009). In this regard, mechanistic models are often able to overcome some of the main issues associated with using ENMs, such as when they are employed to investigate species response to climate change, they are not extrapolating from inferred relationships measured through distribution data but rather aim to translate morphological and physiological traits of a species with key environmental variables and the terrain (Kearney *et al.*, 2008; Kearney and Porter, 2009). This means that mechanistic models require little to no information about the distribution of a species to construct the model (Kearney *et al.*, 2008), which may be much more suited to a pest insect species of which little is known about the origin or geographic distribution but there is the ability to characterize life tables and trait data.

While mechanistic models are not always used for species distributions, they can be projected on to spatial data (e.g. GIS data), like those used as predictor variables in correlative models, to determine the

probability of a given location, or grid cell, to meet the organism's resource requirements (Kearney and Porter, 2004). Information regarding physiological response to climatic variables can be compiled into a framework to understand activity, reproduction and survival thresholds. Mechanistic models that may be most useful for the prediction of pest invertebrate distributions include life history and phenology models (e.g. Gutierrez *et al.*, 2008, 2010, 2012) or thermodynamic niche models (e.g. Kearney *et al.*, 2008; Kearney and Porter, 2009). Like correlative ENMs, they can be interpreted through the Hutchinsonian niche duality, but instead characterize axes of the fundamental Eltonian niche. Mechanistic models can also include information about the microclimate – the environmental conditions an individual of a species will experience and utilize (Kearney *et al.*, 2009).

The downside of using mechanistic models in pest insect species distribution modelling is that this avenue is often data intensive, and thus a single species requires much research attention. This may be possible for established pest species that often have a long history of research interest, resulting in data accumulation (e.g. light brown apple moth, *Epiphyas postvittana* Walker, pine processionary moth, gypsy moth, *Lymantria dispar* L., mosquitoes including *Anopheles* and *Aedes* spp., and others), but not so much for emerging pests that require immediate attention. When sufficient data are available though, mechanistic models are very appropriate and allow for more in-depth analyses of species response to climate change. This is particularly evident for species that are in a state of flux or range expansions (filling potential niche), or through adaptive changes in physiological or morphological traits. Species that are in the process of such adaptive shifts (e.g. the cane toad, *Bufo marinus*) may prove challenging to apply ENMs (Kearney *et al.*, 2008), unless different weightings and model complexity parameters are explored, grounded on other biological information (Elith *et al.*, 2010). This is important in terms of understanding the effects of climate change on pest invertebrates, as research should aim to include

both phenotypic and genotypic flexibility (Bale *et al.*, 2002). Mechanistic models can incorporate levels of variation or plasticity in distribution-limiting traits (Kearney and Porter, 2009; Kearney *et al.*, 2009; Kolbe *et al.*, 2010), which allows for hypotheses of adaptive shifts to be estimated under selective conditions such as climatic change.

Mechanistic models that incorporate trait variability (e.g. Kearney *et al.*, 2009) provide an alternative to using an ENM-centred framework. However, while mechanistic models that characterize the thermodynamic niche (e.g. Kearney *et al.*, 2013) provide comprehensive detail, these require many parameters and extensive empirical research. By having a mechanistic understanding of how climate affects life-history traits such as emergence (e.g. Kearney *et al.*, 2010), and number of generations, it may be possible to translate these into guidelines for control measures. Finally, as they are based on explicit processes, mechanistic models are also able to take directly into account other environmental processes, such as biotic interactions. We talk more about this later.

2.3.3 CLIMEX

One of the most common modelling tools used for pest insect distributions is CLIMEX (Sutherst and Maywald, 1985). This tool uses a process-fitted or semi-mechanistic approach to examine the relationship between climate, species distributions and patterns of growth (Macfadyen and Kriticos, 2012). Importantly, CLIMEX models can be fitted using a combination of empirically measured parameters, abundance and point distribution records. These data types are often complementary for insect pest species and allow for knowledge gaps to be bridged when constructing informative models. Hence, CLIMEX is ideal for modelling distributions of pest insects, as it often is that data are 'patchy' across abundance, distribution information and physiological information (such as life-table studies).

The CLIMEX model works through a series of weekly growth and stress indices

that are combined to produce an ecoclimatic index (EI). The EI describes regions that are unsuitable for the species to persist, through to those that provide a 'perfect' environment for the species. This is interpreted within a scale of 0–100 (Olfert *et al.*, 2011), with an EI over 20 considered to convey ideal conditions (Sutherst *et al.*, 2004) and below 10 an unfavourable environment, though rating interpretations will be species specific to some extent. The strength of CLIMEX lies in its ability to project models to new environments without relationships between variables confounding projections. CLIMEX also has a lot of flexibility; for example, when abundance patterns are not well known, they can be inferred from development rate experiments or observations and these become methods of validation (Kocmánková *et al.*, 2011; Macfadyen and Kriticos, 2012).

The coupling of demographic parameters with spatial distribution information and other different data types gives CLIMEX certain advantages over SDMs and allows for basic physiological information (e.g. response to temperature, moisture) to be incorporated into climate change projections. CLIMEX is able to avoid some of the issues involved with transferability associated with ENMs, due to the model being built on climate change data rather than being extrapolated. This makes CLIMEX suited to predicting new geographical regions for invasive invertebrate species, and also responses to climate change. However, the stress indices are normally derived from the realized distribution and, due to the nature of the climate data used, CLIMEX models do not capture microclimate effects. In this way, CLIMEX is closer to a correlative approach, an important consideration when employing this model type.

Another advantage to using CLIMEX is that it is also able to investigate evolutionary adaptation indirectly by adjusting parameters based on information about changes in physiological tolerances. For example, Hill *et al.* (2014) looked at the mosquito vector of Dengue fever, *Aedes albopictus*, and incorporated different physiological profiles (based on experimental data on adaptive change) to examine how the species might respond to climate change given a shift in temperature tolerance.

2.3.4 Other models

Besides the main types we have just presented, there is a range of other models available to model insect pests and their response to climate change. One that looks particularly applicable is the Insect Life Cycle Modeling (ILCYM) software (Sporleder *et al.*, 2009), which can be used to determine the number of generations in a given geographical area under different climatic conditions (Kroschel *et al.*, 2013). A phenology model like ILCYM could determine if suitable climate space determined by ENM methods would translate into faster population growth for different pest insect species. This coupling of methods would provide some valuable insight into pest insect species and climate change.

As climate change is likely to affect processes beyond what any one modelling process can capture, it may be important to combine multiple modelling methods (e.g. ENM, semi-mechanistic, phenological and thermodynamic mechanistic models). Using combinations of models to assess the response of pest insects to climate change may translate into more targeted management decisions. For example, using CLIMEX alongside ENMs allows for areas of congruence to be assessed (e.g. Lozier and Mills, 2011; Hill *et al.*, 2014).

2.4 Current Developments/Future Directions

So far in this chapter, we have considered species in isolation, and without considering dispersal ability. Both the interactions with other species and the ability of species to move both actively and passively are likely to play major roles in determining response to climate change. Here, we review current developments in each of these categories and suggest ways in which they may be

incorporated in predictive modelling of pest insect species.

2.4.1 Biotic interactions

One of the main limitations when applying SDMs to a single species is that each species is considered in isolation and as a single population. Species, of course, do not exist free from interactions with other species, nor are they homogeneous in response to environmental stressors. Interactions such as competition, predation and parasitism are all likely to be impacted by climate change, resulting in species composition shifts and biocontrol failures (Sutherst *et al.*, 2007; Thomson *et al.*, 2010). Ecologists increasingly recognize the importance of species interactions for mediating the effects of climate change (reviewed in Tylianakis *et al.*, 2008; Gilman *et al.*, 2010; Walther, 2010; Yang and Rudolf, 2010).

Biotic interactions (e.g. competition and predation) may restrict the spread of pest invertebrate species (i.e. a new predator encountered in an invasive range, or competitive interactions between species) under present climatic conditions, but these interactions may mismatch through shift under climate change, resulting in altered pest invertebrate distributions. Biotic interactions also impact on population abundance across time, limiting species distributions spatially. In terms of biocontrol, beneficial (predators and parasitoids) species may respond to climate change in completely different ways than the pest invertebrate they attack (Thomson *et al.*, 2010). Thus, the influence of biotic interactions and their success under a changing climate needs to be considered, and at what spatial scale these interactions are important. For instance, it may be argued that for some species models that incorporate broad climatic variables, biotic interactions may not be important in shaping the distribution at that scale, only at a finer, landscape level. Further, some pest insect species are highly successful competitors and biotic interactions are unlikely to limit distributions outside their

native range (e.g. *Bactrocera invadens*; Hill and Terblanche, 2014).

Incorporating interactions in species distribution models has proved a challenging area of research. Species interactions are currently incorporated in ENMs at a basic level, including covariates of competitive interactions (Pellissier *et al.*, 2010; Meineri *et al.*, 2012) and available prey items (Hof *et al.*, 2012), to look at how these interactions affect modelling outcomes. Another approach that looks promising is to nest a community of species spatially within a modelling framework that incorporates co-occurrence indices (Boulangeat *et al.*, 2012). Population processes such as dynamic ranges and dispersal parameters can also be incorporated into ENMs. Developments in this area include dynamic range models (DRMs) to estimate spatial population dynamics (Pagel and Schurr, 2012; Schurr *et al.*, 2012) and other dynamic species distribution models that can incorporate stochastic processes such as dispersal, growth and competition within a Bayesian framework (Marion *et al.*, 2012). Processes such as biotic interactions and dispersal could also be linked explicitly within a mechanistic modelling framework, and there are simple interaction parameters available for CLIMEX models to examine changes in the EI under climate change (Sutherst *et al.*, 2007).

In considering pest invertebrates and climate change, it is important to consider the types of biotic interactions that may play a role in shaping responses. These may include competition, natural enemies' interactions and host shifts. Some of the avenues for incorporating biotic interactions within SDM frameworks are presented in Kissling *et al.* (2012), highlighting an exciting area of SDM research that will enhance greatly climate change predictions for pest insect species.

Competition

The varying success with which a pest invertebrate species outcompetes endemic and/or other pest species has implications for predicting distributions accurately, both currently and under climate change. The

potential importance of competition in determining distributions is demonstrated by the highly successful invasive ladybird beetle, *Harmonia axyridis* (Pallas), where its success in interspecific competition is implicated in adverse ecological impacts through North America and Europe (Roy *et al.*, 2012). Further, the thrips species, *Frankliniella occidentalis* (Pergande), is a highly invasive pest that has spread from its original range (the western states of the USA) to a worldwide distribution. Despite this, it is largely absent in the eastern states, where a native thrips, *Frankliniella tritici* (Fitch), successfully outcompetes in larval competition (Paini *et al.*, 2008). While there are currently limited examples for pest insects, there are some recent studies looking to incorporate competition into SDM, particularly ENM, approaches. For example, Brame and Stigall (2014) used ENM modelling to reconstruct ecological niches for 11 genera of marine invertebrates over geological time and found taxa adjusted to increased competition by altering aspects of their niche. These types of studies may serve as valuable road maps for incorporating competition into climate change predictions for insect pests.

Predators/parasitoids or natural enemies

The impact of predators and parasitoids on invertebrate pests is well documented, and the presence or absence of natural enemies has been demonstrated to exert a controlling influence on pest insect species distributions (Thomson *et al.*, 2010; Culik *et al.*, 2013). In the absence of parasitism, a mechanistic SDM predicted a wide geographic istribution of glassy-winged sharpshooter (*Homalodisca vitripennis* (Germar)) in the USA and Mexico. Including the interaction with its egg parasitoids (*Gonatocerus ashmeadi* Girault and *Gonatocerus triguttatus* Girault) in the model changed distribution predictions (and abundance) dramatically (Gutierrez *et al.*, 2011). In a well-studied species, more complex interactions may present themselves; for example, parasitoid attacks may induce different host immune responses, and some parasitoids may also make facultative response by adjusting life-history

parameters. Larvae of the moth *Lobesia botrana* (Denis & Schiffermuller) can accelerate their development rapidly and reach maturity earlier in response to cues perceived at a distance from parasitoids. Such a phenotypically plastic life-history shift, induced by the perception of deadly enemies in the environment, is likely to be an adaptive defensive strategy to prevent parasitoid attack, and has important implications in host–parasite dynamics (Vogelweith *et al.*, 2013). A possible corollary of range shift moving from parasitoids extends to phenological change; loss of the cue allows longer development time of the moth. As hosts that mature earlier are smaller, which is often correlated with low fecundity and reduced longevity, maybe this is an advantage in a new environment, whether range change or invasion. Marini *et al.* (2013), in a long-term study aimed at identifying the role of predation and parasitism on bark beetles, concluded a limited effect. These kinds of complex interactions are largely unconsidered for pest insect SDMs, although they comprise key components in understanding the response to climate change and provide many opportunities for future research.

2.4.2 Dispersal ability

Further improvements to species distribution modelling may come from including dispersal information to examine how this influences response to climate change. Currently, most SDMs assume no dispersal, or unrestricted scenarios (see Travis *et al.*, 2013), while others attempt to combine dispersal information to SDMs through process-based modelling approaches (see Elith and Leathwick, 2009, for examples). For pest insect species, dispersal may be in either passive or active forms and play a major role in shaping the distribution. Dispersal may also introduce new species interactions, further highlighting the importance of movement of species as an important component to understand response to climate change properly. Newer methods such as DRMs, as presented in Schurr *et al.*

(2012), are able to incorporate dynamic processes such as dispersal and look promising for pest insect SDMs. Similar to this, population processes are likely to be useful for pest insect distribution modelling (Fordham *et al.*, 2013).

Current implementation of dispersal in pest insect distribution models includes the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand), an invasive threat to North America (Fitzpatrick *et al.*, 2012). In this study, dynamic dispersal was combined with population processes and maps, characterizing heterogeneity in climate and habitat. Fitzpatrick *et al.* (2012) found that simulations generally matched the observed current extent of the invasion of HWA, but were not able to predict accurately when HWA was observed to arrive at different geographic regions. Differences between the modelled and observed dynamics were attributed to an inability to capture the timing and direction of long-distance dispersal events, which substantially affected the ensuing pattern of spread. Other weather events such as increased cyclones or high winds may increase dispersal beyond current conditions for some pests. Such events are inherently difficult to capture using current SDM techniques and corresponding meteorological information.

2.4.3 Genetic diversity

Another avenue to improve pest invertebrate SDM predictions is to incorporate relevant genetic diversity into the models. For example, ENMs typically assume that species exist as one large population, and therefore do not include potentially important difference responses between populations. If species distribution models are applied where clear structure exists between populations (for example, geographic barriers or multiple and distinct introductions), then it could be beneficial to examine the differences in environments occupied by populations or lineages (e.g. Arteaga *et al.*, 2011; Newman and Rissler, 2011). This can be achieved by identifying unique populations

through measures of genetic divergence and partitioning model data into corresponding subsets, or perhaps information on dispersal and movement abilities of a species. While it is possible to measure population structure and divergence using microsatellites, for example, neutral genetic diversity and adaptive genetic diversity are often not correlated (Holderegger *et al.*, 2006). This implies that adaptive niche shifts that may alter response to climate change are not likely to be detected in such population genetic studies; instead, these studies provide information to calibrate modelling procedures around genetic diversity.

2.5 Enhancing Model Predictions with Niche-limiting Traits

As was pointed out when discussing the advantages of CLIMEX, data for pest insect species are often incomplete across the different knowledge domains (e.g. distribution information, physiological studies, demographic studies). A useful approach to predicting the effect of climate change on pest insect species may be to measure niche-limiting traits and then couple this with distribution information to detect variance and/or shifts and how they may influence potential response. We feel this is a framework that will prove to be more successful and draws from different knowledge realms in an insightful way. When applied appropriately, the different types of species distribution models are able to generate hypotheses about the niche of an organism, and then direct further research towards understanding traits that limit the niche (Rey *et al.*, 2012; Hill *et al.*, 2013). Adaptation in limiting traits may lead to niche shifts and mediate a species response to climate change (Chown *et al.*, 2010; Hoffmann and Sgrò, 2011). For the mosquito, *Aedes aegyptii*, Kearney *et al.* (2009) identified egg desiccation resistance as limiting the inland distribution of the species and incorporated this into a model predicting how adaptation in this trait could facilitate range expansion under climate change. Thus, one of the great

challenges is to determine which traits may be limiting current distributions (Wiens, 2011) and then to measure these to incorporate them into predictions. Further, adaptation or persistence in changing environments may also be mediated through phenotypic plasticity: rapid phenotypic adjustment to environmental variation (see Chown and Terblanche, 2006). For invasive species, studies that measure traits in both native and invasive ranges, and across a range of environmental gradients, would be extremely beneficial, though are rare (Alexander and Edwards, 2010). The key traits that are relevant to niche shifts during invasion and under climate change are likely to be:

1. Thermal tolerance: maximum and minimum temperature limits for activity and survival. As temperature plays a large part in determining the niche of a species (Bale *et al.*, 2002), understanding thermal tolerance traits can help to determine species–environment relationships (Terblanche *et al.*, 2006). Thermal tolerance traits are used widely to investigate ecological and evolutionary processes for terrestrial arthropods (Hoffmann *et al.*, 2005; Terblanche *et al.*, 2006; Mitchell and Hoffmann, 2010; Alford *et al.*, 2012). Species often exhibit differences in thermal tolerance limits across environmental gradients, including elevation and latitude (Gaston and Chown, 1999; Hoffmann *et al.*, 2005), with variation across latitude, including phenotypic plasticity, more evident for lower than upper limits of terrestrial arthropods (Hoffmann *et al.*, 2005; Terblanche *et al.*, 2006; Alford *et al.*, 2012; Hoffmann *et al.*, 2013).

2. Desiccation resistance: water loss potential. For terrestrial arthropods, their small size and high surface-to-volume ratio means they are susceptible to desiccation (Johnson *et al.*, 2011). Variation in desiccation resistance has been linked to distributional patterns (Kellermann *et al.*, 2009). For example, tropical species of *Drosophila* have low desiccation resistance (and low heritability of this resistance), compared to widely distributed *Drosophila* species (Kellermann *et al.*, 2009; Hoffmann and Sgrò, 2011).

3. Photoperiodism: physiological reaction to day or night length. While day length will not be affected by climate change, photoperiodism interacts with temperature and varies across latitude, to initiate lipid storage and diapause with the onset of winter (van Asch and Visser, 2007; Lehmann *et al.*, 2012; Urbanski *et al.*, 2012). Adaptation in photoperiodic response has allowed the mosquito, *A. albopictus*, to undergo range expansion in North America (Urbanski *et al.*, 2012). Adaptations in photoperiodic traits may also facilitate earlier emergence (to coincide with milder winter temperatures) and increase herbivore damage under climate change (van Asch and Visser, 2007).

Photoperiodism can underlie different development patterns in a pest, which may facilitate population growth with changed temperature beyond what can be predicted with temperature modelling. Development times greater than explained by temperature differences in *L. botrana* in north-east Italy are interpreted as a means to ensure best fit of the moth to environmental conditions (Pavan *et al.*, 2013).

Whereas mechanistic models can directly incorporate variation in niche-limiting traits, correlative models can determine which environmental covariates may be most important to the niche and which may limit the distribution of species across a geographic range. These can lead to hypotheses about which traits are likely to govern the distribution of the species and should be investigated empirically (e.g. Banta *et al.*, 2012; Hill *et al.*, 2013). This provides an opportunity to use correlative models in tandem with experiments to measure these traits, rather than building full mechanistic models, which can be time-consuming. Alternatively, a few niche-limiting traits for pest invertebrate species could be used with distribution information in CLIMEX-like models that are able to draw from multiple knowledge domains (Macfadyen and Kriticos, 2012).

For some pest insect species, it may be useful to characterize traits for other life stages, such as diapause, and look at intergenerational effects. This could form a

comparison to ENMs and be projected on to the same future climate surfaces (e.g. the CliMond data set) to examine areas of model congruence.

2.6 Conclusion

Different pest insect species will respond to climate change in different ways. Species distribution models can provide important first steps in establishing hypotheses around the niche of a species, to drive hypotheses and experimental work for providing robust advice to managers and agricultural workers in the management of pests and global climate change. The type of distribution model to be employed should be based on data availability – combining from different knowledge domains where possible. When there is comprehensive and unbiased locality sampling, the increasing availability of interpolated weather station data facilitates approximation of the species realized niche using ENMs. Experimentally derived evidence allows for mechanistic models to predict response to climate change through an estimation of fundamental niche axes. The extensive data required are not always available, so tools such as CLIMEX allow for combination across data types. Generally, combining physiological, abundance and distribution data is likely to give better predictive ability.

Through measuring traits such as thermal tolerance, desiccation resistance and photoperiodism and combining this with model (e.g. ENM) predictions, valuable insights into species niche dimensions, and the added potential to investigate adaptive shifts, informs on species response to climate change.

Consideration of other drivers that shape species distributions, including biotic interaction such as competition, the presence of natural enemies and impacts of host shifts, have the potential to increase the accuracy of prediction. Predicting response to climate change for pest insect species will benefit greatly from advances in species distribution modelling to include knowledge of species dispersal ability and interactions, though all SDM work must serve as a guide to inform rather than determine management decisions under climate change.

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