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The Challenge of Modelling and Mapping the Future Distribution and Impact of Invasive Alien Species

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Abstract

Invasions from alien species can jeopardize the economic, environmental or social benefits derived from biological systems. Biosecurity measures seek to protect those systems from accidental or intentional introductions of species that might become injurious. Pest risk maps convey how the probability of invasion by an alien species or the potential consequences of that invasion vary spatially. These maps inform strategic and tactical decisions for invasive species management. Pest risk modellers must contend with the challenges of developing models that forecast the course or consequence of invasions and are more meaningful than could be obtained by chance, of demonstrating the validity of those models and of portraying results on maps in ways that will be useful for decision makers. Frequently, these forecasts depend on extrapolations from limited information to project how a species might be affected, for example, by changes in commerce, exposure to novel environments or associations with new dispersal vectors, or how these species might affect resident species or ecological processes. Consequently, pest risk maps often focus on one phase of the invasion process: arrival, establishment, spread or impact. Risk assessors use different analytical tools and information sources to address each phase. To be certain that pest risk models and maps are fully fit for purpose, models and maps must be critically evaluated at each stage of the development process. Invariably, errors will be revealed. The International Pest Risk Mapping Workgroup has offered a number of suggestions to improve the development of pest risk models and maps. In addition, short-term improvements are likely to be achieved through critical, objective assessments of model performance and greater transparency about model development.

Introduction to Pest Risk Maps

Abraham Maslow (1943) proposed a hierarchy of human needs to explain preconditions for certain human behaviours. Higher-level needs (e.g. self-actualization from which reason, creativity and morality emerge) cannot be met until more fundamental needs are satisfied. Modern concepts of biosecurity intertwine the most basal need for food and water to support life with the next most basic need to have safety and security. Indeed, biosecurity describes the measures taken 'to manage risks of infectious disease, quarantined pests, invasive alien species, living modified

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organisms, and biological weapons. ... [M]any of these problems are a subset of the issue of invasive alien species' (Meyerson and Reaser, 2002). Ultimately, biosecurity is intended to protect human health, the environment or the economy from such biological threats. Pest risk maps for invasive alien species are pivotal tools for biosecurity.

Alien species (also known as exotic, non-native, non-indigenous or introduced species) are those species that have been accidentally or intentionally introduced to one or more areas outside their native geographic range but are by no means extraterrestrial. Often, these species are pathogens, plants or animals with a history of being problematic elsewhere in the world. Three dimensions (i.e. space, time and impact) affect whether a species is considered an invasive alien. In the USA, Executive Order 13112 defines an invasive alien species as 'with respect to a particular ecosystem, any species, including its seeds, eggs, spores, or other biological material capable of propagating that species, that is not native to that ecosystem' and 'whose introduction does or is likely to cause economic harm or harm to human health' (The White House, 1999). International Standards for Phytosanitary Measures similarly recognize a quarantine pest as 'any species, strain or biotype of plant, animal, or pathogenic agent injurious to plants or plant products' that is 'of potential economic [or environmental] importance to the area endangered thereby and not yet present there, or present but not widely distributed and being officially controlled' (FAO, 2012). Both definitions implicitly acknowledge that being alien is insufficient evidence by itself to consider a species an invasive pest.

Pest risk for invasive alien species refers to both: (i) the probability that a species will arrive, establish and spread (i.e. successfully invade) within an area; and (ii) the magnitude of harm should the invasion be successful (Orr *et al.*, 1993; Ebbels, 2003). Economic harms result from lowered yields, reduced marketability, lost trade opportunities or increased management costs. Environmental harms include altered ecosystem functioning (e.g. fire regimes or nutrient cycling) or reductions in the abundance or diversity of resident taxa. Environmental harms can also occur if management activities affect non-target species (e.g. through drift of pesticides or predation by non-specific biological control agents). Environmental harms are considered particularly severe if threatened or endangered species might be affected. Social harms can occur if an invasive species or management activities interfere with benefits people draw from an ecosystem. However, it is not reasonable to assume an invasive alien species will be present in all places at all times; thus, risks posed by invasive alien species have spatial and temporal contexts.

Pest risk maps convey how risks from invasive alien species vary spatially within an area of concern and reflect underlying models of the factors that govern the course of invasion and the effects of invasive alien species on the structure or function of ecosystems (Venette *et al.*, 2010). Some of these models are derived from heuristic descriptions of conditions necessary for an alien species to complete each phase of an invasion or have an impact. Other empirically based, statistical models infer quantitative relationships between a response variable (e.g. the probability of pest arrival) and a number of covariates (i.e. independent or predictor variables). Conceptual mathematical models follow a logical formalism to deduce relationships among variables (e.g. factors that affect species' spread rates). Many models for pest risk maps are based on more general ecological theories about factors that affect species' distributions, rates and patterns of spread, or the outcome of species' interactions. Although the goal of a pest risk map is to characterize how the probability and consequences of invasion by an alien species vary within an area of concern, in practice, pest risk maps frequently address just one or a few components of pest risk. For example, a map could focus on the suitability of the climate for pest establishment within an area of concern, with the rationale that a species which fails to find a suitable climate

cannot establish, spread or have a lasting impact.

A well-crafted risk map serves a number of purposes. From a pragmatic perspective, risk maps can be powerful tools to help managers (e.g. foresters, farmers, pest-survey coordinators and some policy makers) select appropriate strategies and tactics with which to mitigate species' risks. Such risk mitigation (i.e. biosecurity) strategies can be classified broadly as prevention, eradication, suppression and restoration, which correspond generally with the arrival, establishment, spread and impact of invasive alien species (Venette and Koch, 2009). Pest risk maps also inspire critical thought about: (i) the adequacy of current theory, models and data to characterize risks from biological invasions; and (ii) alternative explanations for the course of an invasion or the impacts that have been realized, as was suggested by Koch (2011) for maps of human disease. This chapter describes long-standing goals for pest risk maps and introduces the general process by which pest risk maps are created. General models that have been applied to address different stages of the invasion process are briefly discussed. Types of errors associated with many pest risk models are presented and discussed with respect to measures of model performance. The chapter concludes with a series of recommendations that would help to improve the future development of pest risk models and maps.

An Historical Example of a Pest Risk Map

No consensus exists about when the first modern pest risk map was created. Figure 1.1 is likely among the first maps that begin to address contemporary concepts of pest risk, although the map was not created with the formal definition of pest risk in mind. In the 1870s, the San Jose scale, currently *Quadraspidiotus perniciosus*, was detected in North America for the first time in California's San Jose Valley (Howard and

Marlatt, 1896). The pernicious insect, now recognized as native to parts of Asia, feeds on several deciduous fruit trees, such as peaches, plums, apples and pears, and is easily moved on nursery stock. Few details have been published about the creation of this map, but two pragmatic questions seem to have motivated its production: where was the insect likely to spread within the USA and what major fruit production regions might be affected?

This map (Fig. 1.1), published in 1896, shows the distribution of San Jose scale up to that time relative to 'life zones' in the conterminous USA. The life zones had been proposed by C.H. Meriam to distinguish areas that were especially suitable, or unsuitable, for many plants and animals. Meriam's map identifies five major zones in North America: boreal, transition, upper austral, lower austral and tropical. Known occurrences of San Jose scale seemed to occur 'within or near the so called austral life zones' (Howard and Marlatt, 1896, p. 33). The supposition at the time was that San Jose scale should be able to continue to spread within these regions wherever suitable hosts occurred. The map was developed before modern quarantine regulations were in place, so it was intended to reassure fruit producers in New England and portions of Pennsylvania, New York, Michigan and Wisconsin that the insect would 'not establish itself to any serious extent' (Howard and Marlatt, 1896, p. 35). At the time the map was published, Howard and Marlatt (1896) cautioned about the uncertainty in this forecast by acknowledging that 'its possibility is suggested by what we know up to the present time. Against its probability may be urged the fact that, in general, scale insects … are seldom restricted by geographical limitations which hold with other insects' (Howard and Marlatt, 1896, p. 35). The precautionary note has proven justified. San Jose scale is now established in all conterminous states except Wyoming, North Dakota, South Dakota and Maine (CABI, 1986), but is often kept under control by a suite of natural enemies (Flanders, 1960).

Fig. 1.1. An early 'pest risk' map – the historical distribution of San Jose scale (black dots) in the conterminous USA relative to C.H. Meriam's life zones. (Reproduced from Howard and Marlatt, 1896.)

The General Challenge for Pest Risk Assessors

Pest risk modellers and mappers face a three-part challenge. The first part of the challenge is to develop a model that gives a more meaningful forecast of the course and consequence of a biological invasion than would be obtained by random chance or from obvious, intuitive models (e.g. a plant pest will occur and cause damage anywhere its host plants occur). Models are often needed for species that have not yet arrived in an area of concern. In these cases, pest risk modellers cannot develop or test models with empirical observations on the distribution, biology or behaviour of a species within the area of concern. They must extrapolate from what is known about a species in its native or adventive (i.e. areas where it has invaded) range, from studies in biosecure laboratories or from inferences drawn from taxonomically related species. Further, most pest modellers must rely on a

simplifying assumption that individuals in an invading population are equivalent to individuals from the native range and will be equivalent to future generations (i.e. no significant genotypic or phenotypic changes have occurred or will occur). If an invasive alien species has arrived within an area of concern, initial observations of distribution, dynamics or impact may test the robustness of current knowledge or provide the foundation for a new model.

The second part of the challenge is to demonstrate the validity of the pest risk map and the underlying model. All models (physical, conceptual, statistical or mathematical) are an abstraction of reality. They are never intended to incorporate all of reality. Rather, models are intended to capture enough reality to be useful. What constitutes enough or useful is often a matter of debate. Venette (Chapter 15 in this volume) provides a typology of validity, drawn from the social sciences, to apply to pest risk maps. One might reasonably

consider the map to be a hypothesis, so the validity of the model would be demonstrated though empirical testing (i.e. comparisons of model outputs with observations that are independent of the model). Such evaluation would also formally confirm that the first challenge was met. However, in many cases, relevant empirical observations are likely to be rare or non-existent, at least in the short term. So, pest risk modellers must use other lines of reasoning to argue for model validity. In some cases, arguments for or against a model reduce to so-called first principles with respect to content or construct validity. First principles are axiomatic statements about forces that drive biological invasions, affect population dynamics or affect invasion outcomes. Given the imperfect state of knowledge about biological invasions, debates based on first-principle arguments are seldom resolved, except in the most extreme cases.

Once a model is created and its validity established, the third part of the challenge is to portray results in a way that will be useful for decision making. The risk mapper must consider the required geographic extent (e.g. continent, country, region or parcel) and resolution of the map. Resolution (i.e. grain) refers to the size of grid cells (i.e. pixels) that comprise the map; smaller grid cells provide higher resolution. High-resolution maps can be visually appealing but come with additional uncertainty as fine-scale information is often interpolated from distantly neighbouring observations. Because all maps have some degree of distortion, a consequence of plotting the Earth's curved surface in two dimensions, thought should be given to the appropriate map projection that accurately represents area or distances (DeMers, 1997). Model results should be reported with sufficient precision to support decision making, but should not be so precise as to visually overwhelm the end user (Smans and Estève, 1996). Consider a model output, such as the Ecoclimatic Index from CLIMEX (Sutherst and Maywald, 1985; Sutherst et al., 2007), with values from 0 to 100. At the extreme, each model output could be associated with a unique colour and that

colour scheme applied to the map, but subtle variations among 101 colours may be difficult to distinguish. Typically, all possible model results are divided into classes. For example, Vera et al. (2002) interpret an Ecoclimatic Index of 0 as a climate that is unsuitable for pest establishment; values of 1–10 are marginal; values of 11–25 are suitable; and values >25 are very suitable. A unique colour, stippling or shading is assigned to each class and that classification scheme is applied to each grid cell. For many pest risk maps, red designates the highest-risk areas (i.e. red zones or hot spots).

The Production of Pest Risk Maps

Despite calls for more pluralistic approaches to ecological risk analysis (NRC, 1996), the creation of pest risk maps regularly follows a technocratic approach with distinct roles for assessors, managers and stakeholders. The assessor (i.e. pest risk modeller/mapper or analyst) typically has advanced academic training in entomology, plant pathology, weed science or one of the other core biological disciplines that provide foundational knowledge about taxa that might become invasive alien species (Worner et al., 2014). Assessors may also have experience with computer science or geographic information systems or be asked to collaborate with individuals who do. Formal training in pest risk assessment is rare but is slowly increasing (Worner et al., 2014). Individual assessors or assessment teams have the technical knowledge to produce pest risk models and maps or to evaluate such products from others.

Risk managers are those decision makers, end users or land managers who use pest risk models to mitigate the likelihood or impacts of pest invasion. Risk managers are often senior personnel within governmental agencies. In the ideal case, distinctions between risk assessors and managers are maintained to prevent undue outside pressures from influencing the pest risk model or map. Likewise, risk managers use pest risk models and maps as

components of a much broader decision-making framework.

Stakeholders are those individuals with an interest in the outcome of the risk mitigation decision and are most likely to be affected by that decision. Stakeholders are often given the opportunity to comment on interim or proposed/final pest risk models, maps or mitigation decisions. Stakeholders also have the opportunity to sue in court a government agency if a pest risk model, map or mitigation decision can be shown to cause demonstrable harm. Alternative approaches to ecological risk analysis seek more inclusive roles for stakeholders throughout the process, especially during problem formulation and risk mitigation.

An event, such as a request to import commodities or an incursion by an invasive alien species (as illustrated in the historical example presented above), typically triggers the development of a pest risk map, but the work of the risk assessor begins with problem formulation (Fig. 1.2). In this phase, risk managers and assessors articulate the purpose of the map, identify practical limitations (e.g. budgets and deadlines) and discuss consequences of particular errors. The purpose of the map may dictate whether it is especially important to analyse the arrival, establishment or spread phase of an invasion or to attempt a more integrative analysis across phases. Errors of commission, when some sites are classified as having higher risk than they do in reality, might be acceptable in certain contexts, for example, when risk managers want to know the maximum possible geographic extent of risk. Errors of omission, when some sites are classified as having less risk than they do in reality, might be acceptable to severely resource-constrained decision makers, for example, who are able only to expend resources where needs are greatest. As part of problem formulation, risk assessors evaluate the extent and quality of information about the invasive alien species and the endangered area and identify additional questions for research.

Problem formulation is the most important phase in the production process but is often most neglected because decision makers are not always able to articulate fully how they intend to use a risk map or what would constitute an acceptable end product. The challenge for scientists who are responsible for the production of pest risk maps is to 'balance rigor and timeliness in their work to obtain an acceptable degree of accuracy' in their map for decision makers; for decision makers, 'the challenge is to describe clearly what information is needed to support time-critical decision making' (Venette et al., 2013, p. 1). The urgency for a pest risk map can become especially high when an invasive alien species has been detected within an area of concern and decision makers contemplate needs for quarantine, eradication or containment and consider the potential consequences if no, or ineffective, action is taken.

Once the problem has been fully described, the pest-risk-mapping process moves to the analytical phase (Fig. 1.2). This phase begins with the selection of a model or suite of models appropriate to the task. Numerous software packages, described in the next section, exist to support model development. These packages typically rely on information about an invasive alien species and spatially explicit covariates. This information is more accessible now than it has ever been. For example, several online databases provide current and historical species' distributions, climatological records, elevation data, land-use classifications and population censuses. Nevertheless, not all desired data may be available, so a number of models may be considered but ultimately rejected if the requisite data to forecast the outcome of interest cannot be obtained.

Next, the assessor calibrates the model(s) by estimating key parameters to account for unique aspects of the invasive alien species under consideration or the qualities of the endangered area that has been or might be invaded. In some situations, the assessor calibrates the model by fitting it to a training data set. In the verification step, the assessor checks for coding errors and confirms that the model is giving outputs that are consistent with the data that were used to develop the model. A
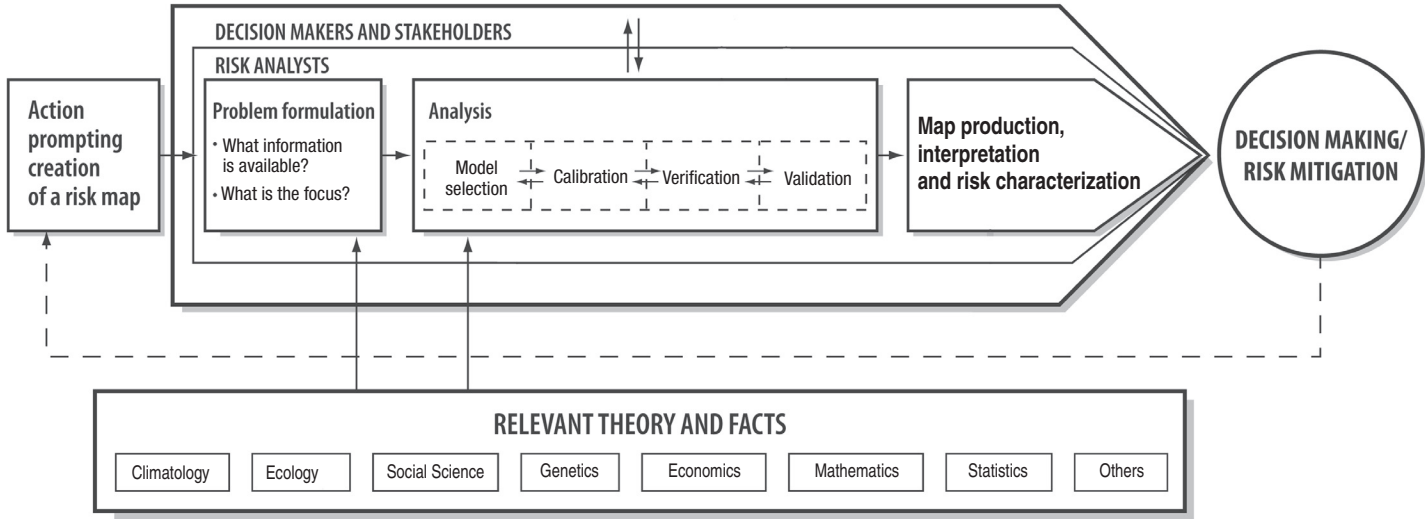
Fig. 1.2. Diagram of the events that lead to the development of a pest risk map. Pest risk analysts communicate with decision makers and stakeholders throughout the process. As the process concludes, models and maps are given to decision makers to select risk mitigation options.

validation step follows. Here, model outputs are compared with a completely independent set of data, sometimes called a test data set. Validation exercises are meant to gauge the reliability of the model. The analysis phase culminates in the production of a pest risk map. Advanced geographic information systems now exist to allow users to create visually compelling map products. These products are used by decision makers to select strategies and tactics to mitigate the risk posed by the invasive alien species. The mitigation decision itself may prompt the development of a new risk map.

An aspirational component to include with the map is a representation of the uncertainty associated with the forecast for each grid cell. Methods to characterize uncertainty in support of decision making have been proposed (e.g. Koch and Yemshanov, Chapter 13 and Yemshanov et al., Chapter 14 in this volume) but are not yet routine. Uncertainty stems from imprecise uses of language (i.e. linguistic uncertainty), a lack of knowledge (i.e. epistemic uncertainty) and inherent variation in a system (i.e. aleatory uncertainty; Regan et al., 2002). Further study of a system can reduce epistemic uncertainty, but can only serve to characterize aleatory uncertainty. Uncertainty assessments for pest risk maps presently address aleatory uncertainty.

Overview of Models to Create Pest Risk Maps

In many respects, pest risk maps take spatially implicit concepts about the course of biological invasions or impacts from invasive alien species and make them spatially explicit. For example, Orr et al. (1993) proposed one of the first qualitative risk assessment models for invasive alien species. The model had two major components, the likelihood of pest invasion and the potential consequences of pest invasion. Each of these components had three to four sub-components. Although the model only required answers of high, medium or low for each of these sub-components, the model asked a number of intrinsically spatial

questions about an alien species or a commodity with which that species might be associated. Where is the species likely to arrive within the area of concern? Where might the species move? Where could the species encounter suitable climate and host plants? Pest risk mappers use a variety of models to provide spatially specific answers to these questions.

Arrival

Arrival (i.e. entry) describes the likelihood that a species could be brought into an area of concern and the conditions under which arrival would occur. Models for arrival are generally intended to answer one or more of the following questions: where is a species most likely to arrive; by what means is it likely to arrive; and in what numbers and condition (i.e. live, moribund or dead) will it arrive? Answers to these questions are typically used to justify biosecurity measures, such as inspecting cargo, screening luggage or prohibiting imports, to prevent the arrival of highly threatening species into an area of concern. Answers may also suggest the futility of such efforts for species that are likely to be brought into an area of concern by natural processes (e.g. with wind or water). When justified, biosecurity strategies that prevent the arrival of a highly threatening species are generally considered the most effective and least costly relative to other biosecurity measures.

A number of models are used to address the arrival of invasive alien species. In general, these models are used to identify particular alien species that should be of concern or to analyse pathways by which those species might arrive within the area of concern. For example, in trait-based screening assessments, a number of characteristics that improve the likelihood that a species will successfully invade a site and cause harm are identified by expert opinion or through statistical analyses of previous invasions. For example, Pheloung et al. (1999) provide an extensive list of characteristics related to the biogeography and

ecology of invasive plants (e.g. evidence that the species has naturalized beyond its native range or produces buoyant propagules). Risk assessors evaluate whether a plant species of concern has these traits and use the results to generate a weed risk assessment score. This index correlates well with experts' perceptions about the degree of risk posed by particular plant species. Similarly, Kolar and Lodge (2002) analyse previous fish invasions to identify characteristics of fish (e.g. relative growth rate, diet breadth, temperature tolerances and previous invasion history) that are associated with (un-) successful invasions and estimate the probability that new fish species will establish, spread or cause harm in the Great Lakes. Such trait-based models typically are not used to generate pest risk maps but frequently rely on risk maps, especially spatial assessments of climate suitability, in the course of the assessment. Screening assessments can also be used to select species for more in-depth analysis.

Pathway models typically focus on the means by which a species might arrive in the area of concern or on the suite or abundance of potentially pestiferous species that might be associated with a particular commodity or conveyance. Pathway models often de-compose the process by which pests/commodities are moved from a country of origin to the area of concern into discrete steps. The probability of successful com-pletion of each step is estimated. For example, Colunga-Garcia and Haack (Chapter 3 in this volume) analyse import trade statistics to determine where bark- and wood-boring insects associated with solid wood packing might first arrive in the USA and be subsequently moved within the country.

In other pathway models, each step in the pathway is characterized by a probability distribution (i.e. a probability-density function). In a process generally known as Monte Carlo analysis, values are selected repeatedly at random in proportion to their likely occurrence as defined by each probability distribution. The values are used to calculate a new probability distribution for the number of individuals that are likely to complete all of the steps and arrive in the

area of concern. For example, Gould *et al.* (2013) studied the potential for *Copitarsia corruda* to arrive in the USA with imports of Peruvian asparagus. In the course of their studies, they developed a model using statistical distributions to describe: (i) the volume of asparagus imported at different times of the year; (ii) potential rates of infestation, i.e. eggs per spear; (iii) proportionate survival of eggs during transport; (iv) the likelihood of disposing of asparagus at importer warehouses, whole-sale distributors or retail outlets; and (v) the potential for individual insects to develop into adults (i.e. moths) by feeding on discarded asparagus. Monte Carlo analysis was used to estimate the likelihood that at least one mating pair of *C. corruda* on Peruvian asparagus would arrive in the USA and escape into the wild (B. Caton, North Carolina, 2014, personal communication). The analysis suggested that the likelihood would be low because once produce moved beyond importation facilities, an insufficient volume of asparagus was present at any point in time for a mating pair to develop.

Although many invasive species have been transported into areas of concern directly through human activities (e.g. international trade), some species, par-ticularly pathogens and small insects, may be transported via wind. Models such as HYSPLIT and PMTRAJ have been used to describe where low-level jet streams might carry species of concern and in what numbers (Parry *et al.*, Chapter 4 in the current volume). These models may also be used to describe the passive spread of a species within the area of concern after the species has established.

Establishment

Establishment occurs when an invasive alien species sustains a population through time by local reproduction. Models for establishment are generally used to determine where a species is most likely to persist through time if it were to arrive, where a species might ultimately spread if given enough time and where a species

might eventually cause economic or multiple harms (Baker *et al.*, Chapter 2 in this volume). For establishment to occur, an invasive alien species must encounter suitable climate, food and a mate and avoid local antagonists (e.g. predators, pathogens and competitors). Maps of potential establishment are useful, for example, to determine the need to eradicate an invading population or to keep the invasive alien species from spreading by enacting quarantines.

Several spatially explicit models to characterize where a pest might establish are known synonymously as bioclimatic envelopes, habitat models, species distribution models or ecological niche models. Frequently these models focus on an analysis of climate because many invasive alien species are ectothermic (i.e. poikilothermic) and temperature directly affects developmental, reproductive and survival rates. Different schemes have been proposed to classify these models. Inductive modelling approaches relate information about a species' geographic distribution, either presence-and-absence or presence-only data, to any number of environmental covariates to infer statistically what factors might explain where a species occurs. Inductive models do not depend on knowledge of mechanisms by which environmental covariates might affect distribution. In contrast, deductive modelling approaches specify factors a priori that should shape species' range limits and abundances and rely on results from appropriately designed studies to evaluate, for example, how changes in temperature will affect population growth rate. Information about the climate at a site (i.e. grid cell) and the relationship between the response and the covariates is used collectively to forecast if a species might persist in the area represented by the grid cell if it were to arrive.

Software to create models for establishment varies considerably. Some software is devoted to a single modelling approach and provides a clear structure for the analysis. Venette *et al.* (2010) identify 13 software packages that have been used to evaluate environmental suitability for establishment.

Two popular inductive models, GARP (genetic algorithm for rule-set prediction) and MAXENT (maximum entropy; e.g. Jarnevich amd Young, Chapter 5 in this volume), ask the user to provide latitudes and longitudes for known occurrences of a species and to select ecologically relevant, geo-referenced covariates, commonly climatological data.

Structured deductive models (e.g. NAPPFAST; Magarey *et al.*, Chapter 6 in this volume) ask the user to provide estimates of key parameters (e.g. upper and lower temperature thresholds for development) from published literature or from appropriately designed experiments. Another software tool, CLIMEX (Sutherst and Maywald, 1985; Sutherst *et al.*, 2007), may be used inductively, deductively or through a combined approach. The software assumes that broken stick models will describe a species' response to temperature or moisture gradients. The challenge is to estimate key parameters for these models. Estimates may be derived from field or laboratory studies (i.e. deductively) or by iteratively altering parameters in the model until a qualitatively satisfactory fit between the model outputs and the known distribution is reached (i.e. inductively).

Other statistical software packages (e.g. R or SAS) provide powerful analytical tools to assess the relationship between species occurrences and covariates but offer little structure to guide the analyses. Venette *et al.* (2010) identify six classes of statistical models that have been used for this purpose.

Another type of inductive model, a self-organizing map (Worner *et al.*, Chapter 7 in this volume), uses information about communities of pest organisms in an area of concern and their similarity to communities around the world to determine which species (and from where) are most likely to establish within the area of concern.

A significant assumption behind many inductive species distribution models is that the species is in equilibrium with its environment and geographic range boundaries are stable. Such a condition is more likely to be true for a species in its native range than in its adventive range.

Inductive models developed from occurrence data in the native range may underestimate the potential distribution of an invasive alien species in the adventive range because the models typically do not explicitly account for the effects of natural enemies. Natural enemies are more likely to constrain a species in its native range than in the adventive range. Freedom from natural enemies is a commonly cited reason for the success of many biological invasions. The constrained distribution from natural enemies in the native range might be misattributed to the effects of climate. Conversely, inductive models developed from a species' adventive range may over-estimate the distribution in a species' native range.

Spread

Spread describes the means by which a species redistributes itself in an area of concern after it has established. Spread models are often used to answer general questions such as: where is the species likely to move through time and when is it likely to get there? Spread is either active (i.e. by flying, walking or swimming) or passive (e.g. wind-, animal- or water-dispersed). Passive, anthropogenic spread occurs when humans intentionally or accidentally move a species to new areas. If spread of an invasive alien species has been extensive before detection occurs or if a species is so highly dispersive that quarantines are unlikely to be effective (e.g. certain wind-borne pathogens), biosecurity measures begin to focus on managing and mitigating damage from the species.

A number of quantitative models have been developed to measure and forecast spread by invasive alien species. This extensive body of literature will not be reviewed here; see Shigesada and Kawasaki (1997) and Hastings *et al.* (2005) for excellent reviews. Many spread models have not been organized into software packages as has been done with species distribution models (but see Robinet *et al.*, Chapter 8 in this volume); most spread models are derived mathematically and key parameters are estimated statistically from empirical observations (e.g. Tobin *et al.*, Chapter 9 in this volume). Geographic information systems can be useful to estimate distances moved over periods of time, the results of which are further analysed in statistical software, and to project the location of the expanding invasion front over time.

In general, many spread models require information about the probability that an individual will move, or be moved, a particular distance (i.e. the dispersal kernel) and quantitative information about life history parameters, particularly population growth rates. Such information is frequently unavailable for species that have only recently been detected in areas outside their native range. Rare long-distance dispersal events have a significant impact on patterns and rates of spread but are difficult to forecast. Gravity models and individual-based models have been used to describe where invasive alien species might be moved, for example, based on an understanding of flows of people and goods through transportation corridors (Prasad *et al.*, 2010; Crespo-Perez *et al.*, 2011; Koch *et al.*, 2011).

An alternative approach, applicable to invasive alien species that have already arrived within the area of concern and started to spread but do not seem to have reached the limits of their distribution, relies on statistical analyses of realized spread. The rationale is that future spread is likely to be similar to previous patterns of spread. Generalized linear models (GLMs) such as logistic regression have been used for this purpose. Care must be taken to account for spatial and temporal auto-correlations in these data or risk misestimating the statistical significance and explanatory power of the resulting model.

Many spread models assume that the propensity of a species to disperse is spatially independent. However, tests of this assumption have found that the likelihood that an individual will move depends on the environment into which it is moving. This phenomenon poses a

significant complication for pest risk modellers because models of spread with parameters estimated from data from one location may have little relevance to spread behaviour in another location (Hastings *et al.*, 2005). For pest risk modellers, extrapolations based on experiences with an invasive alien species in another location or at another time seem inescapable, so results must be interpreted with great caution.

Integrative models of invasion or impact

Integrative models attempt to synthesize results from different data sources or individual models into a more complete characterization of pest risk. For each grid cell, models estimate the probability of an invasive alien species arriving, either directly as a beachhead population or indirectly from other infested sites within the area of concern, and establishing and the associated magnitude of impact. Complete, spatially explicit characterizations of risk are exceptionally difficult to prepare and, as a result, are rare (but see Murray and Brennan, 1998).

Rule-based models (Meentemeyer *et al.*, 2004; Seybold and Downing, 2009), often implemented in geographic information systems, have been used to describe spatial differences in relative degrees of risk. The models are forms of multi-criteria decision models. Rules, often expressed as 'if …, then …' statements, are typically provided by experts to reflect their knowledge and opinions about factors that might contribute to invasion risk or impact. The 'if' describes a condition that would increase or reduce risk and the 'then' typically results in the assignment of a risk score. Often, one gridded data layer relevant to each rule is queried and scores assigned to each grid cell on the map. Resultant scores from each rule for the same grid are summed and the final summation used as an indicator of the degree of risk in that cell. A simple summation indicates that each rule contributes equally to the final risk score. In more complex situations, a weighting factor can be applied to reflect the relative importance of each rule. Weights can be assigned directly by experts or can be elicited through structured questions. For example, the analytical hierarchy process, a form of multi-criteria decision model, provides an elicitation approach to generate these weights.

The weighted sums are quantitative, but ordinal, data and reflect the correct rank order of cells in a data set. The (weighted) sums do not necessarily capture the correct ratio between observations. So, for example, if sites 1, 2 and 3 get sums of 4, 16 and 32, respectively, site 3 has greater risk than sites 1 and 2, but the risk at site 3 is not eight times the risk at site 1 or twice the risk at site 2. Some authors prefer to refer to such scores as semi-quantitative assessments of pest risk.

Periodically, rule-based models will incorporate the results from an arrival, establishment or spread model. A rule is formed for the model output and applied just as it would have had the data been based on empirical observations. However, because the models generate an estimate of the actual value, the model outputs have some degree of error. This error propagates through the model, but only rarely is such error propagation formally measured.

Individual-based models have also been constructed to generate a more comprehensive representation of pest risk. For example, Koch and Smith (2008) describe the potential spread of the ambrosia beetle *Xyleborus glabratus* in the south-eastern USA after accounting for the geographic distribution of hosts, the density of hosts, the degree of climate similarity to regions in Asia where the beetle is native, the expected spread rate and the effect of host density on spread. This well-integrated model does not attempt to forecast the potential impact of the beetle and its fungal symbiont *Raffaelea lauricola* on potentially affected host plants.

Impacts from invasive alien species remain exceptionally difficult to forecast quantitatively (Venette *et al.*, 2010). In general, impacts depend on the response of resident species or genotypes to the invasive alien, and those responses are likely to vary depending on the densities the invasive

alien pest can achieve. For example, the detection of a single individual may trigger international quarantines on potentially affected hosts and cause severe economic impacts. Partial budgeting, which can be performed in any spreadsheet, is a relatively simple technique to estimate the net effect on farm incomes from value of lost yield (e.g. volume of timber or tonnes of grain) and increased control costs, less any additional revenue or cost savings (Soliman *et al.*, 2010). Such impact assessments work well at the micro scale, but do not capture potential macroeconomic impacts, such as shifts in market prices or consumer demand. However, it is not yet clear whether these effects can be mapped.

Model Performance

Risk modellers can rigorously evaluate the performance of a model by comparing outputs with independent observations from the field. In the calibration phase of model development (see 'The Production of Pest Risk Maps' above), such comparisons are useful to determine if model parameter estimates are appropriate and during the validation phase, to evaluate the quality of a model's forecasts. A 2 × 2 decision matrix (i.e. confusion matrix; Table 1.1) is one approach to compare model outputs and field observations when the model gives a binary result (e.g. species presence or absence). Cell A includes the true negatives, cases when a model suggests that an event will not happen and it does not. Cell B describes instances where the model suggests an event will occur, but in actuality it does not. These circumstances are known as type I errors, false positives or commission errors. Cell C describes instances when the

model indicates no event will occur but it does. These are type II errors, false negatives or omission errors. Cell D includes the true positives, cases where the model suggests the event will occur and it does. Overall model accuracy is the proportion of all cases in which the model correctly forecast the outcome: $(A + D)/(A + B + C + D)$. Specificity is the proportion of observed non-events that were correctly indicated by the model: $A/(A + B)$. Sensitivity is the proportion of events that were correctly identified by the model: $D/(C + D)$.

Sensitivity can receive considerable attention in the development of pest risk models and maps for two primary reasons. First, greater confidence is placed in the observance of events than non-events (i.e. not seeing anything). Detecting and recognizing an event (e.g. a species is present) is empirically testable. For example, specimens can be examined for the accuracy of identification and new specimens can be collected to confirm initial reports. For non-events, the adage 'you can never prove a negative' is appropriate. To conclude that no event of interest has occurred and will not ever occur at a location implies a great deal of knowledge about current and future events. For newly arrived alien invasive species, in particular, it may be more accurate to conclude that a species has not arrived at a site yet than to conclude that it has not arrived. Second, decision makers frequently consider false positives to be more acceptable than false negatives. The reason for this bias is not completely clear, but studies of risk perceptions in humans consistently indicate that the fear of loss is greater than the fear of a missed gain.

If events are trusted over non-events and false positives are preferable to false negatives in pest risk analysis, pest risk

Table 1.1. Confusion matrix for the comparison of binary model outputs with independent field results.

Model output	Field results	
	No event	Event
No event	A. True negatives	C. False negatives
Event	B. False positives	D. True positives

models and maps may overestimate the potential distribution and impact from invasive alien species. Models that forecast a more widespread occurrence of an alien invasive species will be judged superior to models that forecast a more limited distribution. In fact, the simplest model, 'the invasive alien species will be everywhere', will have perfect sensitivity now and in the future. Overestimation increases the likelihood that an area will be covered by biosecurity measures. If resources for biosecurity are allowed to vary 'as needed', overestimation may lead to unnecessary biosecurity measures and a suboptimal allocation of resources to other valued goods and services. Alternatively, if resources are fixed, overestimation may lead to resources being spread too thin.

In cases where model specificity is a concern, the potential for overfitting a model becomes an issue (Peterson *et al.*, 2011). Overfitting describes the case where an excessive number of covariates, more than can be justified statistically, are included in a model. Overfit models will often suggest that an invasive alien species has specific environmental requirements and will not be able to survive in areas other than those it currently occupies. Overfitting is not easily recognized a priori but is revealed during model validation. Models found to have low error during the verification stage but high error when tested on an independent data set are likely to be overfit (Peterson *et al.*, 2011). Such models lack robustness and are likely to underestimate the area potentially affected by an invasive alien species over time.

Many risk models describe the potential for future events as a probability, not as an absolute yes or no. In these cases, the analyst must select a threshold to describe when an event is probable (e.g. when the probability is >50%) or when it is not. At very low threshold values, the model will have perfect sensitivity but no specificity. Conversely, at high threshold values, the model will have perfect specificity but no sensitivity. A receiver-operating characteristic (ROC) curve describes the trade-off between model sensitivity (i.e. the true positive rate) and the false positive rate (i.e. 100 – specificity). If a model has no discriminatory power, the ROC curve will fall along the diagonal and the area under the ROC curve (AUC) will be 0.5. As the discriminatory power of the model improves, the AUC will approach 1. AUC is not appropriate to evaluate models of potential distribution (Jimenez-Valverde, 2012). Alternatives to AUC have been proposed when only presence data are available (Phillips and Elith, 2010; Li and Guo, 2013).

Conclusions

The International Pest Risk Mapping Workgroup (IPRMW) offered pragmatic recommendations to address pressing issues for the production of pest risk maps (Venette *et al.*, 2010). The IPRMW now includes nearly 90 scientists, modellers and decision makers from around the world who specialize in aspects of pest risk analysis. Most members have formal or informal affiliations with decision-making bodies that regulate the movement of plants, plant products or pests that might affect plants. Some recommendations were intended to support ongoing pest risk analysis efforts. Species' distributions and environmental covariates are still frequently lacking, so a call was made to expand the availability and accessibility of primary data sources. In addition, greater communication between pest risk analysts and decision makers is needed to clarify interpretation and uses of risk maps. Some recommendations called for changes of practice within the pest risk modelling and mapping community. For example, calls were made for pest risk modellers to more fully document model development and validation, improve representations of uncertainty, increase international collaborations and work towards pest risk maps that include impacts. Some recommendations were intended to support new individuals coming into the discipline. General needs were recognized for a best-practice guide, a modelling tool kit and advanced training in risk modelling practice. Lastly, a call was made to incorporate global

climate change and studies of human behaviour into pest risk models.

Pest risk analysts must also contend with some pressing issues in basic science. Foremost, many risk assessment models do not account for evolution in the invading population or recipient communities. In fact, the assumption is that phenotypic traits remain constant. This simplifying assumption constrains most risk models to relatively short time horizons (e.g. <30 years). Critical questions pertain to the heritability and conservation of the fundamental niche, selection for resilience to environmental stresses and the evolution of increased competitive ability (Felker-Quinn *et al.*, 2003; Wiens *et al.*, 2010; Morey *et al.*, 2013). Pest risk analysis has been criticized for failing to account for post-invasion evolution by alien species (Whitney and Gabler, 2008).

Pest risk modelling and mapping occurs at the interface of science and policy. Some nations may perceive governmental actions to protect human, animal and plant health from risks posed by invasive alien species as non-tariff barriers to free trade. The World Trade Organization's Agreement on the Application of Sanitary and Phytosanitary Measures (also known as the SPS Agreement) defines principles for the appropriate implementation of such protective measures (WTO, 1994). Devorshak (2012) provides a thorough discussion of the history of the SPS Agreement and its current and future ramifications for plant health protection. A chief principle of the SPS Agreement is that nations have the sovereign right to implement biosecurity policies and practices as they deem necessary insofar as those measures are supported by scientific evidence, are consistent with international standards and are not a disguised barrier to trade. The sovereignty principle acknowledges that no nation or body can dictate the biosecurity measures taken by another nation. Similarly, although the methods described in this text have been scrutinized for scientific credibility during the peer review process, no nation or organization is obligated to use these approaches.

Common challenges for pest risk modellers and mappers are outlined in this chapter and some solutions are offered throughout the remaining text of this book. These solutions (i.e. modelling approaches and software tools) were developed out of necessity and have proven to be scientifically credible. However, these tools could be refined or new tools developed to address long-standing concerns over risks posed by invasive alien species. By making the conceptual and logistical challenges that underlie pest risk mapping more transparent, my hope is that others may see new opportunities for scientific and technical advancements.

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