

Pest Risk Maps for Invasive Alien Species: A Roadmap for Improvement

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Pest risk maps are powerful visual communication tools to describe where invasive alien species might arrive, establish, spread, or cause harmful impacts. These maps inform strategic and tactical pest management decisions, such as potential restrictions on international trade or the design of pest surveys and domestic quarantines. Diverse methods are available to create pest risk maps, and can potentially yield different depictions of risk for the same species. Inherent uncertainties about the biology of the invader, future climate conditions, and species interactions further complicate map interpretation. If multiple maps are available, risk managers must choose how to incorporate the various representations of risk into their decisionmaking process, and may make significant errors if they misunderstand what each map portrays. This article describes the need for pest risk maps, compares pest risk mapping methods, and recommends future research to improve such important decision-support tools.

Keywords: biological invasions, biosecurity, ecological niche models, climate change, pest risk assessment

Strategic and tactical decisions for the management of invasive alien species depend on accurate spatial and temporal characterizations of pest risk. Options for managing biological invasions include prevention, eradication, containment, and suppression (reviewed in Venette and Koch 2009). For decisionmakers to determine whether management is needed, and, if so, which option is most appropriate, they must know the potential for a species to bring harmful ecological, economic, or social impacts to places outside its native range. Those species with some potential to cause harm in an area of concern are considered to be “pests,” and analysts can estimate this potential through pest risk assessment (FAO 2007). Pest risk describes (a) the likelihood that a species will successfully invade an area, and (b) the magnitude of resulting harm. Thus, a complete risk assessment relies on underlying models and their projections of species entry, establishment, spread, and impact within an area of interest. For invasive alien species that are not yet present in an area of concern, or that are present but have a limited distribution, the models should provide timely insights about the potential geographic range and impact the species might have—without waiting for those effects to be realized. Maps of endangered areas provide a powerful means of communicating spatial patterns in

these estimates (FAO 2007), but these maps are simply visual representations of underlying models that help to characterize pest risk.

Producing models that contribute to the estimation of pest risk poses daunting challenges to risk analysts and researchers. How does one reliably estimate the potential distribution and harmful impacts of a species that has never before been present in an area of concern? What environmental, ecological, and evolutionary factors must be considered? What are the consequences of ignoring or oversimplifying certain factors or processes? Given that little or no empirical data about the species in the threatened area may be available, what other sources of information might be suitable surrogates? How do information needs and sources change as the spatial scale of the assessment changes (e.g., from entire continents to small parcels of land)? These questions define broad avenues for future research because answers thus far remain largely subjective, often debated, and typically untested.

The idealized process for developing a pest risk map (figure 1) begins with an action, such as a new pest incursion, a proposed change in international trade, or the recognition of a species as a biosecurity threat. This event leads to a detailed formulation of the problem, which includes an extensive search for information regarding the species and

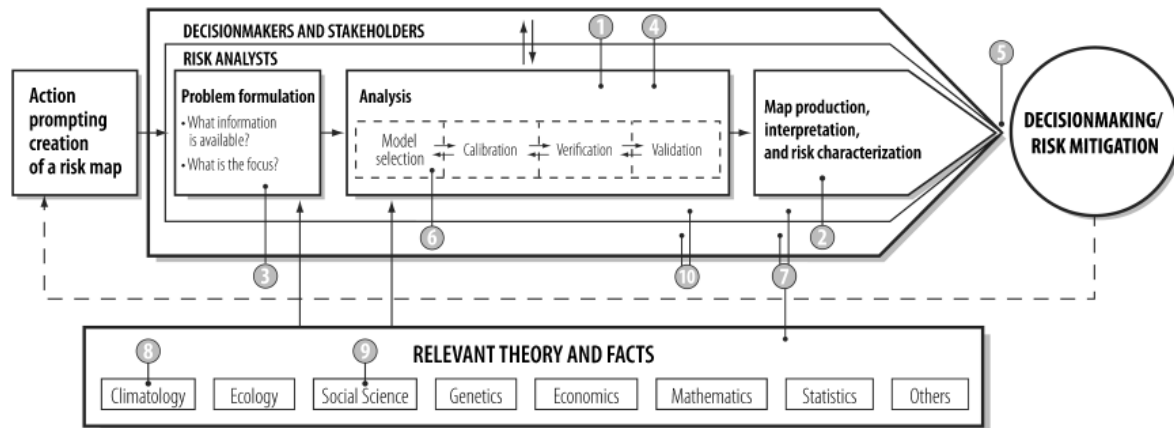


Figure 1. Conceptual diagram of events that lead to the development of a pest risk map for invasive alien species. Risk analysts maintain communication with decisionmakers and stakeholders throughout the process. As the process completes, models and maps are provided to decisionmakers who are responsible for risk-mitigation decisions. Numbers correspond to recommendations for improvements provided in the text.

endangered area. Choices are made about whether the goal of the model should be to assess the probability of invasion, the consequences of invasion, or both, given the available information. The problem-formulation step also involves careful discussions with decisionmakers and stakeholders and should be informed by relevant theories and information from the broader research community (e.g., climatology, ecology, economics, social science, etc.).

In the analysis phase, one or more models are selected, calibrated, verified to satisfy underlying assumptions, and validated against independent data. Previous research provides insights on factors that should be included in the model, potential model performance, and methods of validation. Additional models may be considered if initial selections do not perform well. Finally, results are depicted on one or more maps and interpreted relative to the uncertainty in the models. Throughout the process, the analyst maintains communication with stakeholders and decisionmakers. The final products are given to a decisionmaker to assist in selecting risk-mitigation measures that will reduce the probability of pest entry and establishment and maximize prospects for an effective response should these events occur. Risk-mitigation measures could include, for example, the passage of appropriate phytosanitary regulations, allocation of resources to respond to the event, establishment of pest-surveillance networks, or the development of effective diagnostic capabilities. In some cases, especially when a number of possible projections have been produced, the mitigation decision itself may prompt a new round of analysis.

Ideally, a pest risk model and map would address the probability and consequences of invasion, both of which are required for a pest risk assessment (FAO 2007). In practice, models have been used primarily to identify areas where a species is most likely to enter, establish, or spread, evaluating one or more these outcomes in isolation or in aggregate. These models and maps inform components of a pest risk

assessment but are not complete assessments per se. However, models and maps that describe the potential suitability of environments for pest establishment are especially important because if a pest arrives in an area that is unsuitable for establishment, it poses little risk. Climatic suitability also sets bounds on future spread (e.g., Pitt et al. 2009).

Models of the potential distribution of an invasive alien species in an area of concern are now relatively easy to produce. Computers with sufficient computational power to perform extensive analyses are inexpensive and accessible. Geographic information systems now have the capacity to process complex spatial data sets. Numerous ecological niche models are now available to relate biotic and abiotic conditions to the probability of a species being present at a site (Kriticos and Randall 2001, Peterson and Vieglais 2001, Hirzel and Le Lay 2008). Global environmental databases, many in digital format, are now more readily available than they were in the past, and information about species' geographic distributions is more accurate and more extensive. Collectively, these advancements have facilitated the development of pest risk models and maps, but questions surround how models and maps should be made and interpreted. Different objectives, assumptions, modeling approaches, and underlying data lead to different pest risk maps (figure 2). Indiscriminate model selection may cause incorrect estimates of invasive alien species' potential ranges and inaccurate assessments of pest risk. Consequently, decisionmakers may select the wrong mitigation measure and over- or underinvest in that strategy.

Figure 2 shows three pest risk maps for *Phytophthora ramorum*, an invasive alien pathogen responsible for several plant diseases in Europe and the United States. The maps were prompted at different times, either when *P. ramorum* was identified as the cause of tanoak (*Lithocarpus densiflorus*) and oak (*Quercus* spp.) mortality in California and Oregon, or when the pathogen moved across the United

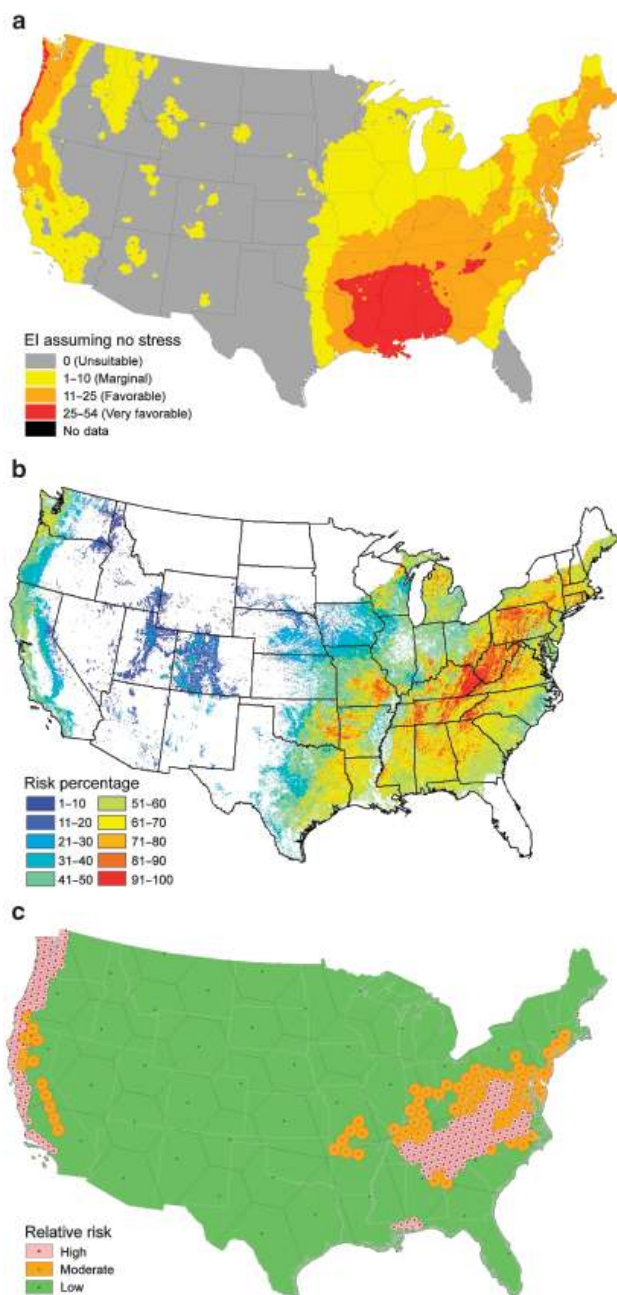


Figure 2. Pest risk maps for *Phytophthora ramorum*, the pathogen responsible for sudden oak death, reflecting the results of (a) a CLIMEX model describing climatic suitability for infection and growth (Venette and Cohen 2006), (b) a NAPPFAST model and expert rule to measure the relative likelihood of the pathogen encountering suitable hosts and climate for infection (Magarey et al. 2007), and (c) an expert-driven rule set characterizing the relative risk of pathogen arrival and establishment (USDA 2004).

States in infected nursery stock. All three maps relate to the probability of the pathogen's invasion into the conterminous United States and provide guidance on where to survey, but they offer no estimate of the pathogen's potential consequences. The models underlying the maps incorporate

different factors because the analysts making them had different perspectives on the importance of each factor relative to the quality of available data about it. Figure 2a illustrates the relative suitability of the climate for *P. ramorum* establishment based on output from the model CLIMEX (Venette and Cohen 2006). Figure 2b provides a relative index that integrates potential host density with output data from the NAPPFAST model of winter survival and climate suitability for *P. ramorum* infection (Magarey et al. 2007). Figure 2c gives a general index of the potential arrival of the pathogen on *Rhododendron* species nursery stock, suitability of climate for establishment, and presence of a subset of hosts based on an expert-driven, rule-based model (USDA 2004). These maps have several similarities, particularly with respect to no- or low-risk estimates for much of the western United States, but differ in the estimated extent and pattern of "some" risk, particularly for the eastern half of the country. These differences affect practical decisions about the necessary extent of early-detection surveys, especially in most Gulf Coast states.

This article is the result of the first meeting of the International Pest Risk Mapping Workgroup, convened by the US Department of Agriculture (USDA) Animal and Plant Health Inspection Service in June 2007. Twenty-two professionals from Australia, New Zealand, Canada, the United States, England, and Norway, with close connections to research and regulatory communities for invasive alien species, met to review recent advances in pest risk mapping approaches, provide general recommendations for such mapping, and chart a course to improve future risk maps. In this article, we place pest risk maps in a historical context and review common approaches behind their development. We explain the relationship between these approaches and similar methods applied to native species. Finally, we report our key recommendations to improve pest risk mapping procedures and products. We hope that these recommendations will help pest risk managers produce better estimates of the spatial dynamics and impacts of invasive alien species, broaden our understanding of the processes that underlie biological invasions, and improve communications about pest risk models and maps.

Historical context for modern pest risk maps

Pest risk maps have their foundation in fundamental ecological concepts that address factors governing species' distribution and abundance. For example, the Sprengel-Liebig law of the minimum explains that the environmental resource in shortest supply limits population growth (reviewed in van der Ploeg et al. 1999). Shelford's law of tolerance expands this tenet for each environmental resource by incorporating a lower and upper bound at which population growth starts and stops, respectively; a narrower optimal range in which population growth is maximized occurs between the two bounds (reviewed in Shelford 1963). If a resource falls outside the optimal range but within the lower and upper bounds, it limits population growth and is subject to the

constraints of the Sprengel-Liebig law. These laws typically apply to abiotic resources, such as heat, light, or nutrients, and do not explicitly consider the interactions a species may have with resident taxa.

The relative importance of density-dependent (e.g., interspecific and intraspecific interactions) and density-independent (e.g., climatic) factors on population dynamics has been a long-standing source of academic debate. In the late 1850s, for example, Darwin emphasized the role of competition in determining the fitness of individuals, while Wallace advocated that less-fit individuals are eliminated because of environmental adversity (reviewed in Bulmer 2005). In the 1950s, Nicholson contended that variations in population size and distribution were determined predominantly by density-dependent feedback mechanisms such as competition, predation, or parasitism (e.g., Nicholson 1954). Nicholson's contemporaries, Andrewartha and Birch (1954), believed that environmental stochasticity was the main factor affecting population size and distribution. At the 22nd Cold Spring Harbor Symposium in 1957, the groups came face to face, but no consensus was reached (MacArthur 1960). Elements of the debate resurfaced when Davis and colleagues (1998) experimentally demonstrated that two fruit fly species would expand their temperature range (*sensu* Shelford) if competitors were removed. However, while recognizing that species interactions are important in the field, Hodkinson (1999) and Baker and colleagues (2000) argued that experiments in confined spaces are likely to overestimate species interactions because they do not provide the heterogeneous habitats that allow fauna, such as these two *Drosophila* species, to coexist.

Today, most ecologists acknowledge the significance of both density-dependent and -independent factors for population dynamics. Hutchinson's (1957) concept of niche provides a framework to integrate these factors. Central to this concept are the realized niche and fundamental niche, which describe the *n*-dimensional environmental conditions under which a species can persist in the presence of other species (including natural enemies) and their absence, respectively. In geographic space, the fundamental niche, representing the ecophysiological limits to the persistence of a species, will be more extensive than the realized niche, and the realized niche will always occur within the fundamental niche (Brown et al. 1996).

Most pest risk models attempt to characterize dimensions of a species' fundamental niche (e.g., McKenney et al. 2007). On average, these models tend to perform well over multiple locations, but are less reliable for a specific location. Models that explicitly incorporate density-dependent factors and characterize dimensions of the realized niche may provide better forecasts for a specific location if intra- and interspecific interactions restrict species ranges. Pest risk models that incorporate these interactions are less common because they require substantially more information about the diversity and dynamics of resident taxa and their interactions with an invasive alien

species. This information is not often available over large geographic scales. In addition, the high site specificity of many realized-niche models often precludes application to other geographic areas.

Creation of pest risk maps

The creation of pest risk maps involves many steps. We outline and describe them below.

Requisite information. Knowledge of a species' current distribution is a fundamental building block of most ecological niche models. The primary sources of pest distribution data for modeling purposes are field surveys, museum collections, phytosanitary inspections, literature reports, dedicated pest-distribution databases, and expert opinions. For example, the Pest Information Platform compiles observations from field personnel to provide near real-time distributions for a targeted set of species within the United States (Isard et al. 2006). Similarly, the Global Biodiversity Information Facility (www.gbif.org) allows users to download data from a large number of museums and sources worldwide.

Access to numerous databases unfortunately does not ensure acquisition of adequate data for model construction. Primary sources typically provide presence information, but in most cases specimens and their locality information were collected without the intention of generating a model or map. Records are vulnerable to epistemic uncertainty caused by incomplete or inadequate information or linguistic uncertainty caused by misinterpretation of the available information (Regan et al. 2002). For example, a record may not indicate whether a specimen came from a self-sustaining population or from a few individuals recently brought by cargo or wind. Distribution records do not always specify the local abundance of the species, or whether specimens were alive or dead at the time of collection—both indicators of the suitability of an environment for a species. Likewise, a specimen's reported location may be misleadingly vague if the place name is common to a city, county, and state. Often, specimen records are not linked to voucher specimens, so their identity cannot be subsequently verified. Related to this is the ongoing process of taxonomic revision leading to species' name changes. Such potential geographic, taxonomic, and epistemic uncertainties could have critical negative impacts on models derived from such records.

Secondary sources of information, such as pest information sheets, literature reviews, literature databases, and compilation maps, summarize information from primary sources. These data may create new challenges if primary sources are misinterpreted or if only coarse geographic information is reported. In some cases, important details that are necessary to evaluate the veracity of the records are lost during collation. Coarse descriptors of geographic distribution—for example, at a national or regional level—are often useless for many modeling techniques that associate environmental variables with the probability that a species is present in an area.

Recently, some species surveys have started to report absence information—areas where a deliberate search was conducted but the species was not found (e.g., Kriticos et al. 2007). Details of the intensity of the search in space and time and the sensitivity of sampling methods become critically important (Venette et al. 2002). “Absence” as a mere consequence of never having looked for a species, or of a species never having had an opportunity to arrive in an area, indicates little about the potential for establishment within that area.

In addition to empirical observations of a species in space and time, ecological niche models may be driven by a more basic understanding of the direct effects of environmental gradients on population processes for a species of interest. For example, developmental and reproductive rates of poikilotherms depend on exposures to temperatures over time (often measured in units of degree days) above a minimum threshold (Jarvis and Baker 2001). To estimate areas where establishment of an organism may be precluded, managers have used knowledge of the number of degree days an organism might accumulate in an area and how many it needs to complete its life cycle. Knowledge of population responses to environmental stressors (e.g., cold, heat, etc.) is needed to estimate establishment if the number of degree days in an area is adequate for a species to complete its life cycle.

Time series data that describe fluctuations in population densities are infrequently used to evaluate the impacts of climate on the presence or abundance of invasive alien species. Time series data collected at multiple locations might provide unique insights that mere presence and absence data cannot, especially with respect to the relative importance of density-dependent or density-independent effects, although we know of few instances where this approach has been applied.

Pest risk models also require spatially explicit data (i.e., covariates) that describe environmental conditions within the area of interest. Global data (measured and processed in a consistent way) are needed so that analyses within and outside the species’ current distribution are possible. Global measurements of temperature, precipitation, and elevation, for example, satisfy these criteria and are often used.

A common problem is that critical biological and environmental data for invasive alien species are not available in areas where they are most needed. For example, the global distribution and abundance of potential host plants for invasive alien herbivores are not available. More important, data describing the distribution and abundance of invasive alien species in their native ranges are often poorly cataloged and exist in a form not readily available to the broader research community. Furthermore, in regions where investment in instrumentation infrastructure has been lacking, facilities such as weather stations may be limited. In both cases, it is difficult to develop reliable models that relate species occurrence to environmental covariates. The lack of instrumentation infrastructure is also problematic when analysts begin to apply pest risk models.

Model selection. Numerous approaches are available to model the potential distribution of species with respect to climate or other variables. Many researchers have described and compared these approaches (Guisan and Zimmermann 2000, Kriticos and Randall 2001, Baker 2002, Worner 2002, Elith et al. 2006). Table 1 provides a brief description of some common approaches but excludes many process-oriented models developed for specific insects or plant pathogens (e.g., GMPHEN for gypsy moth, *Lymantria dispar*; Sheehan 1992).

The approaches in table 1 are designed to describe the relationship between environmental covariates and the potential occurrence of a species, but they differ considerably in their underlying philosophy, particularly with respect to whether an inductive, deductive, or combined process is used to determine the relationship (Sutherland et al. 1995). Deductive approaches use detailed knowledge of climatic preferences determined from laboratory studies to infer where a species can occur. Inductive approaches use statistical analyses of the known distribution of a species and climatic data to estimate its climatic preferences. Some modeling approaches, such as CLIMEX, NAPPFAST, or expert-driven rule sets, are flexible enough to use deductive or inductive methods to determine relationships between the presence of a species and environmental covariates. Pitt and colleagues (2009) used an expert-driven rule set to classify the suitability of different land-cover classifications for the Argentine ant, *Linepithema humile*, in New Zealand (inductive rules; figure 3a), distinguish categories based on average annual degree days accumulated above 15.9 degrees Celsius (deductive rules; figure 3b), and combine these factors into an index of habitat suitability (figure 3c). Regardless of how the relationships between environmental covariates and species presence were determined, their application to a landscape follows deductive reasoning.

Inductive approaches to determine the relationship between environmental covariates and the occurrence of an invasive alien species require less knowledge of a species’ biology; they can rapidly provide pest risk maps for coordinated surveillance, control, and communication in response to a pest incursion. The results of inductive approaches may also suggest complex interactions between a species and its environment (Worner 2002). However, variables and parameters should be supported biologically rather than purely statistically (Harvey et al. 1983); otherwise, inductive methods run the risk of becoming mere modeling exercises without deepening our understanding of the factors that affect population processes. In particular, without rigorous validation, inductive methods run the danger of “overfitting” the underlying relationships between environmental variables and species occurrence, and predicting that the species will be found only in areas proximal to where it currently occurs. Inductive approaches also run the danger of unintentionally ascribing other variation in a landscape to climate. For example, Beale and colleagues (2008) found a poor association between climate and European bird

Table 1. Common approaches used to predict species distributions based on an inductive or deductive understanding of the influence of environmental conditions on populations.

| Approach | Description | Inductive or deductive |
|--------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------|
| Artificial Neural Networks (ANN) | General modeling technique based on machine learning | I |
| BIOCLIM/ANUCLIM | Climate pattern-matching with minimum bounding rectangle (MBR) | I |
| BioMOD | Applies the four most widely used modeling techniques in species predictions, namely Generalized Linear Models (GLM), Generalized Additive Models (GAM), Classification and Regression Tree analysis (CART), and ANN | I |
| CART (Classification and Regression Trees) | General statistical procedure for defining set membership based upon environmental correlates | I |
| CLIMATE | Climate pattern-matching with choice of several match techniques, including MBR and point-to-point similarity indices | I |
| CLIMATE ENVELOPE | Climate pattern-matching using MBR | I |
| CLIMEX: Compare locations function | Process-oriented model describing species response to climatic variables and predicting climatic suitability | I/D |
| CLIMEX: Match climates function | Climate pattern-matching procedure generates an index of climatic similarity | I |
| DOMAIN | Climate pattern-matching using a point-to-point similarity index | I |
| ENFA (Ecological Niche Factor Analysis) | Computes suitability functions by comparing the species distributions in ecogeographical variables space with that of the whole set of cells using a multivariate approach | I |
| Expert-driven rule set | Personal opinion about the factors and conditions that determine species presence; often expressed as a series of "if...then" statements | I/D |
| FloraMap | Principal components analysis of monthly climate data using multivariate and Fourier transformation techniques | I |
| GARP | Generates environment-description rules using machine-learning techniques | I |
| GLM/GAM | Generalized linear model/generalized additive model; general statistical procedures for fitting species response functions to survey data | I |
| GRASP | Generalized regression analysis and spatial prediction | I |
| HABITAT | Creates a convex polytope in n -dimensional space | I |
| MaxEnt | Probabilistic machine learning technique based on the distribution of maximum entropy | I |
| NAPPFAST | Online templates for phenology, infection, and empirical models and a climate-matching tool | I/D |
| STASH | Process-oriented model describing species response to climatic variables, and predicting climatic suitability | D |

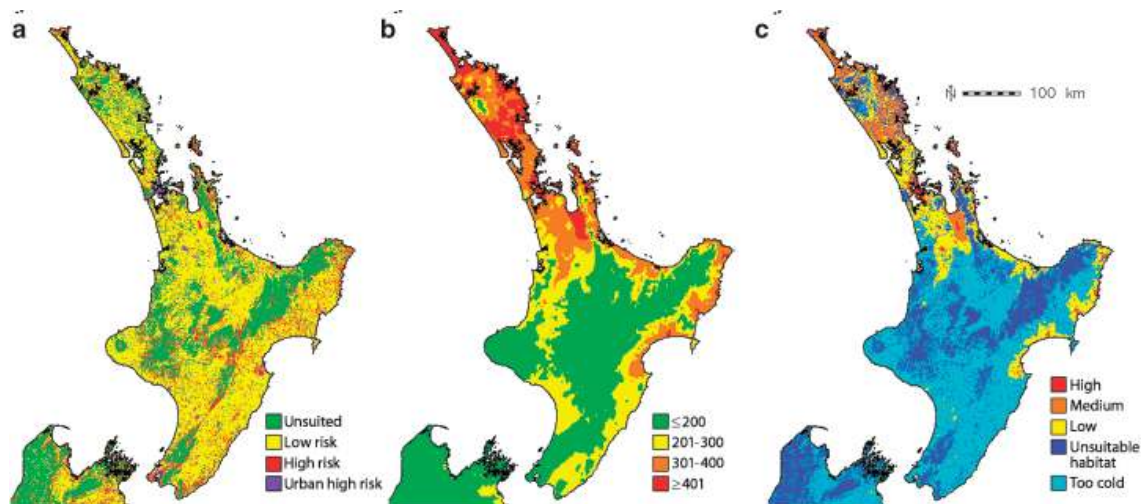


Figure 3. Contributions of expert rules for (a) land cover classifications and (b) annual accumulation of degree days above 15.9 degrees Celsius to estimate (c) habitat suitability for *Linepithema humile*, Argentine ant, in New Zealand. Maps reprinted from Pitt and colleagues (2009) with permission of the Ecological Society of America.

distributions, even though traditional ecological niche models suggested these relationships existed. Bird distributions might be better explained by regional differences in habitat loss, predator removals, agricultural production, or other historical factors (Beale et al. 2008).

Purely deductive approaches have appeal because the information used to develop the forecast is completely independent of observed occurrences of the invasive alien species. Thus, all distribution records can be used to rigorously validate the model. However, deductive approaches may predict a much broader geographic range than will actually be observed if other limiting factors (*sensu* Sprengel-Liebig) are ignored or unknown, or if density-dependent factors are significant. Deductive approaches are unlikely to estimate a smaller geographic range than will be observed.

The methods in table 1 vary considerably in the degree to which their model structures are specified. In some cases (e.g., BIOCLIM [Nix 1986], CLIMEX [Sutherst and Maywald 1985]), the model is sufficiently structured so that environmental tolerances (*sensu* Shelford) can be clearly inferred, and previous experience with the model helps with the interpretation of model results. In other cases (e.g., NAPPFAST; Magarey et al. 2007), the modeling platform gives the user flexibility to specify both model structure and parameters. Other approaches, such as general linear models or general additive models (e.g., Austin and Meyers 1996), classification and regression trees (e.g., Usio et al. 2006), or artificial neural networks (e.g., Gevrey and Worner 2006), are analytical methods with almost no imposed structure, especially with respect to potential covariates under consideration. As the degree of the model's structural freedom increases, it becomes impossible to make generalizations about the applicability or performance of a model for a new species based on previous experiences without a deeper understanding of the specific problem formulation.

Several of these approaches have been used for invasive alien species and noninvasive native species. However, the need to make projections for geographic areas outside the area used to develop the model is a key difference between ecological niche models for invasive alien species and species within their native range. Conceptually, ecological niche models for native species deal with interpolation issues, largely estimating presence and absence among known occurrences. In contrast, ecological niche models for invasive alien species often deal with extrapolation issues, projecting presence and absence for novel environments well beyond locations used for model development. Thus, the relative performance of ecological niche models to estimate distributions of resident taxa (e.g., Elith et al. 2006) has modest relevance when selecting a modeling approach for invasive alien species.

Calibration, validation, and interpretation. Fitting model parameters, verifying model behavior, and testing hypotheses about model performance with the data used to generate the model are integral phases of model development. Inherent

variability in biotic responses to environmental conditions and spatial and temporal variation in those conditions complicate model calibration (also known as parameter fitting). Models are said to be “verified” when results conform to underlying model assumptions.

Once a meaningful model has been developed, it may be validated by comparing its projections with independent data not used for calibration (Jeffers 1988). Often, data sets are stratified to generate a set of independent data for analysis of model behavior, but the method of stratification is significant. Validation is most rigorous when it is based on a biased subset of data that are spatially and climatically distinct from the data that were used to calibrate the model. Such validation provides a more meaningful measure of the transferability of the model to new places or time periods (Phillips 2008). For pest risk models, validation in an area of interest is problematic, particularly in cases where a model projects presence but the species has not been observed. The model may be wrong (a statistical type II error) or the species may simply have not yet arrived.

Pest risk maps must be interpreted with a full understanding of what the map seeks to portray and the assumptions embodied in the underlying model. Maps of the potential distribution of an invasive alien species do not necessarily correspond with the areas where such species will have the greatest impact, or with the areas most likely to be invaded first. Thus, maps often reflect components that contribute to overall pest risk, but not the risk in its entirety.

Error and uncertainty in pest risk maps are inevitable. While imperfect knowledge of complex ecological systems is well recognized, recent studies that compared species-distribution models illustrate model uncertainty well, showing clearly that different models can give divergent results (Elith et al. 2006, Pearson et al. 2006, Araújo and New 2007). Likewise, the same modeling approach, calibrated with different data, can yield different model parameters and characterizations of risk (Kriticos and Randall 2001). For example, CLIMEX gave different results for *Cereus jamaicaru*, a cactus native to Brazil, when climatic tolerances and requirements were inferred from its native distribution alone (figure 4a) or from its native and adventive range in South Africa (figure 4b). Models built on information from the adventive range can provide a clearer indication of the constraints of climate alone on distribution, and may provide more accurate range estimates in other areas where density-dependent constraints are unlikely. Estimation errors could be measured statistically, but no consensus yet exists on a suitable metric to compare projected and observed occurrences for a species that is in the process of invading.

Top recommendations for improved risk maps

The following recommendations are intended to clarify communication about the strengths and limitations of pest risk models and maps, improve the accuracy of these tools, and expand knowledge about the ecology of biological invasions. Numbers reflect the relative priority of the

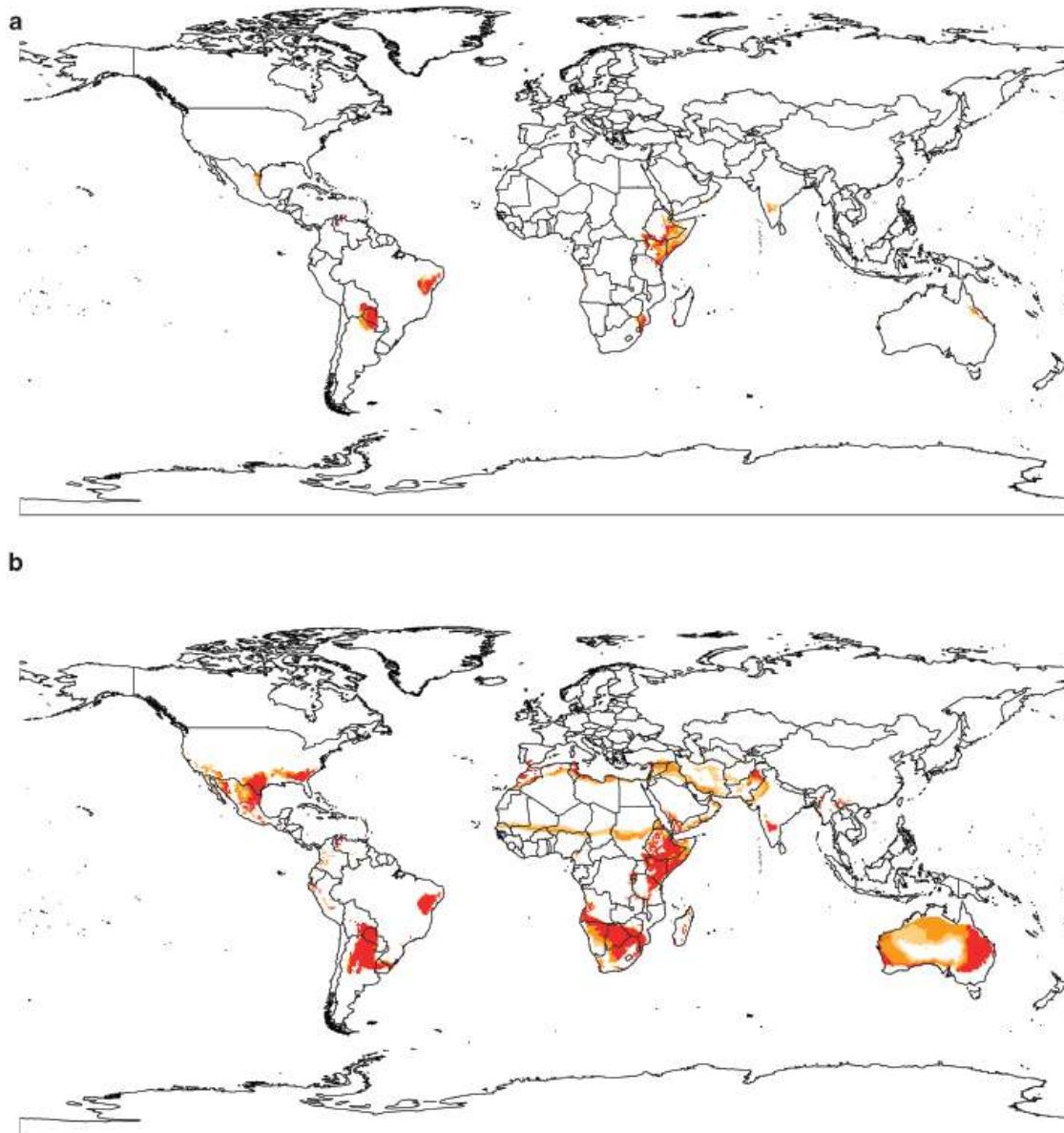


Figure 4. Projected global climate suitability for *Cereus jamaclaru*, a thorny Brazilian cactus, in Australia, based on CLIMEX models calibrated with distribution information from (a) Brazil, the native range, and (b) the native and adventive range in South Africa (Kriticos and Randall 2001).

recommendations among the workgroup participants and are used to illustrate where the recommendations may affect the pest-risk-mapping process (figure 1).

1. Provide greater documentation of model development and assessment. It is critical that risk analysts document the rationale and procedures for model selection, calibration, verification, and validation. Such documentation will help stakeholders, decisionmakers, and researchers evaluate the veracity of the model, and help the model stimulate testable hypotheses. Analysts should also provide a clear statement of the intent of the risk map and the justification for the modeling approach, explicitly documenting all assumptions and expert judgments, and

ideally assigning degrees of belief (i.e., subjective probabilities) to those judgments (FAO 2007). Analysts should also clearly explain calibration procedures. Currently, details of presence data are often well described, but absence data may not be. Many inductive approaches (table 1) generate pseudo-absence data (or background data, *sensu* Phillips 2008) by randomly selecting points that are not known to contain the species of interest and treating them as absent in the analysis. Pseudo-absence data are as influential as presence data in modeling. Any use of pseudo-absence data should be clearly documented, and the analyst should indicate the methods by which these data were generated (e.g., selected at random within political or ecological boundaries).

The analyst should consider as many sources of verification (*sensu* Jeffers 1988) and “reasonability checks” as possible. For example, phenological observations for a set of locations might be used. Where there are inconsistencies between different data sources, the likely possible explanations for the inconsistencies need to be discussed for the target audience.

The analyst should describe the model validation methodology with care, including the steps used to maintain independence of the calibration and validation data sets. In the case of widely dispersed pests, this could involve model calibration and verification with one range of continents, and validation with data from another range (Kriticos and Randall 2001). Generally, statistical tests of model performance are preferred to qualitative comparisons of model output and known occurrences, but there are limitations to many goodness-of-fit measures (Lobo et al. 2008, Peterson et al. 2008). Thus, several measures of performance are desirable.

As a final assessment step, pest risk maps should be compared, at least qualitatively, to other pest risk maps developed for the same species (e.g., Sutherst and Bourne 2009). In fact, many pest risk maps have barely acknowledged previous analyses. Formal statistical comparisons of maps from different authors are extremely rare. Intensive comparisons of different models using the same data inputs to address the same question provide a means for analysts to gain a better appreciation of the relative merits and characteristics of different modeling approaches, and they help decisionmakers select a single model.

2. Improve representation of uncertainty. Uncertainty is inherent in pest risk models. However, for many pests, the immediacy of the threat to natural or agricultural resources requires agencies or scientists to develop a model despite substantial uncertainty about the ecosystems in the pest’s native range or those it might occupy in the future (Regan et al. 2002). While many pest risk analysts implicitly acknowledge uncertainty in their analyses (e.g., adopting a simple ordinal-scale risk-rating system rather than a specific probabilistic one), there is no standard method for communicating uncertainty to other scientists, policymakers, regulators, or the public. With respect to pest risk models and mapping for invasive alien species, few have attempted to statistically identify the sources of uncertainty that can make such models unreliable. Lack of validation and absence of uncertainty assessment are serious issues for such models and indeed for all ecological modeling (Fielding and Bell 1997, Elith et al. 2002).

Uncertainty in risk maps may derive from the input parameters, the model used to represent the system of interest, or the presentation of model outputs. Parametric uncertainty may develop from measurement and systematic errors, incomplete or sparse data, natural variability in the system, or subjective judgment in the estimation of parameter values (Elith et al. 2002, Regan et al. 2002, Barry and Elith

2006). Model uncertainty arises from the way in which the model is constructed; that is, its underlying assumptions as well as its algorithmic components (Barry and Elith 2006). Uncertainty also arises from the selection of variables and processes considered critical to risk, which are thus included in the model (Regan et al. 2002). In terms of presentation of outputs, pest risk maps are subject to uncertainties also seen in other types of spatially explicit analyses (e.g., uncertainty due to rescaling, aggregation, generalization, or extrapolation of inputs). Uncertainty often goes unrepresented in pest risk maps, so the maps may be perceived to convey more certainty than actually exists (Woodbury 2003).

Pest risk analysts may take several steps to address uncertainty. Sensitivity analyses or Monte Carlo simulations (Regan et al. 2003, Johnson and Gillingham 2004) measure how robust the projections are in the face of variability and uncertainty in model inputs and structure. Verification and validation provide estimates of model error. Comparisons between models, ensemble modeling, or multimodel inference (e.g., Hartley et al. 2006) may also facilitate assessments of model uncertainty. Bates and Granger (1969) originated the concept of an ensemble forecast and showed that a structured combination of predictions can yield a lower mean error than any individual prediction. Models that contribute to the ensemble forecast result from different initial or boundary conditions, different model parameters or parameter estimates, different model structures or formulations, or combinations of the foregoing (Buizza et al. 2005, Araújo and New 2007). All approaches are designed to represent the uncertainty surrounding model projections and might ultimately generate a probability distribution function, or at the very least a frequency distribution from which confidence limits of some future state of the system potentially could be derived.

Ongoing research is attempting to find new ways to measure uncertainty, represent spatial variation in uncertainty in a map, and evaluate the consequences of uncertainty for decisionmaking. For example, Yemshanov and colleagues (2009) developed a stochastic simulation model to characterize the joint probability (p) of entry, spread, and establishment of an invasive alien woodwasp, *Sirex noctilio*, in each 1-square-kilometer grid cell on a map of eastern North America (figure 5a). The researchers measured uncertainty with the binary entropy value, $H(p)$, which can be used to define upper and lower limits on p (figure 5b).

3. Expand availability and accessibility of primary data. The accessibility of data is of primary importance to modelers. When data are unavailable, pest risk analysts are often forced to rely on expert opinion. However, there is a growing recognition that expert opinion can be extremely biased and misleading. Useful data include pest and host distribution, weather and climate, ecological habitat types, and trade data. Other commonly available data layers such as elevation and land use can also be valuable. Thanks to advances in remote sensing and spatial modeling using

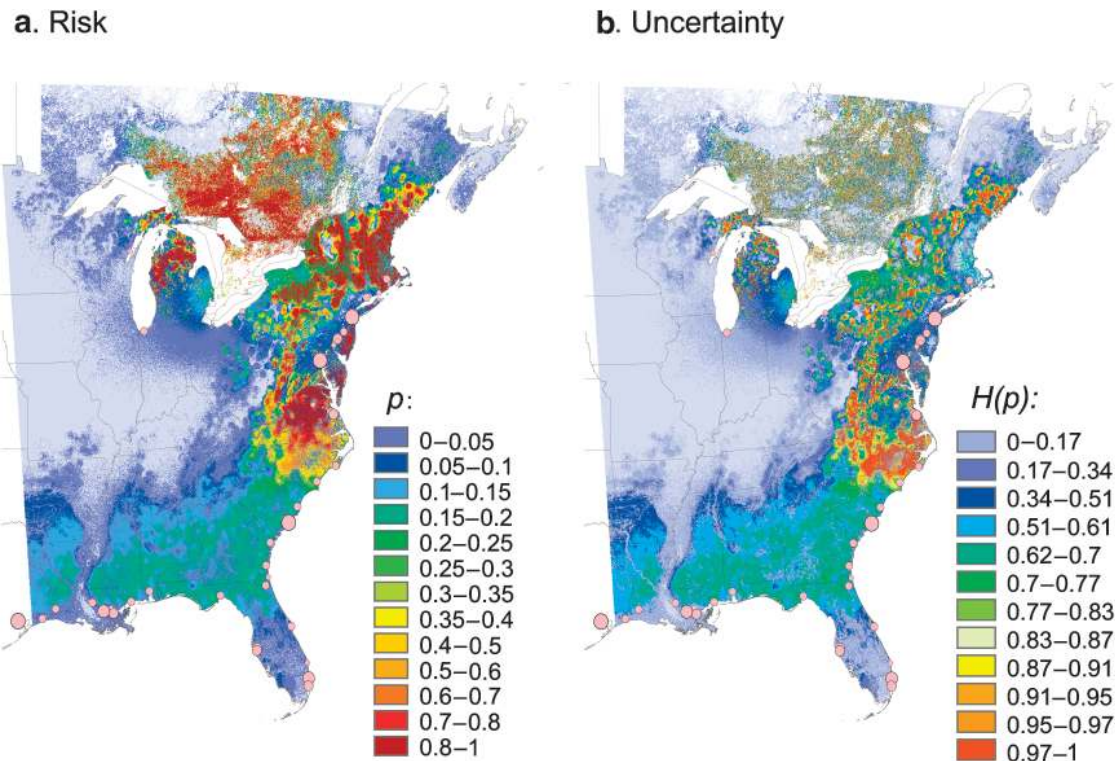


Figure 5. Results of a stochastic simulation model for *Sirex noctilio*, a Eurasian woodwasp, in eastern North America describing (a) the joint probability of successful entry, spread, and establishment, p , assuming imports increase at 3% per year, and (b) the uncertainty in p , based on the binary entropy value, $H(p)$. Uncertainty is greater as p gets closer to 0.5. Pink dots indicate ports of entry, and the size of the dot indicates the relative amount of host material that enters a port. Additional model details can be found in Yemshanov and colleagues (2009).

geographic information systems, there has been an explosion of available data in recent years, and this trend will probably continue. However, even when data are available, quality should not be taken for granted. Analysts should explicitly note concerns and implications regarding measurement or interpolation errors, georeferencing accuracy, identification, and nomenclature when describing their procedures and products.

4. Develop a best-practice guide and tool kit for modeling. A best-practice guide would be helpful in building risk models and creating risk maps. Such a guide could identify common pitfalls and recommend steps to overcome problems, especially with respect to data sources and availability, model and parameter selection, metadata, and documentation; map output; and treatment of uncertainty. The guide would not endorse any particular modeling approach or software package. Although a recent book on species distribution modeling (Stockwell 2006) covers many best-practice topics, including data collection, spatial analysis, and error measurements, it cannot be used as a practical guide for invasive alien species because of the unique challenges invasive alien species present (e.g., range expansion in the absence of natural enemies).

5. Expand communications with decisionmakers on the interpretation and use of risk maps. Risk communication is possibly the most overlooked part of risk mapping. One issue is the actual presentation of maps, where poor choices in the map's layout, scale, colors, categories, and depicted results can create confusion or lead to misinterpretation (Monmonier 1996). A second issue is the manner in which the analyst conveys technical aspects of the pest risk model to decisionmakers. On one hand, as we have recommended above, it is important for analysts to discuss all their assumptions, explain the algorithms they used, and describe the quality of the data on which their models are based. On the other hand, decisionmakers frequently prefer succinct answers that facilitate the making of timely, often urgent, decisions. Effectively communicating the true meaning of risk maps and the desired level of methodological detail is likely to be an ongoing issue for both parties.

Communication will be especially challenging if decisionmakers prefer to use only one map to represent risk. Both parties benefit from the awareness that pest risk maps are just one factor in the decisionmaking process (Pielke and Conant 2003). Better decisions are made when risk managers consider all factors affecting the decision (e.g., stakeholders, institutions, perspectives, values, and resources), rather than

pest risk maps alone. Risk map users should also assess other criteria for evaluating the quality of projections including modeling purpose, model accuracy, model sophistication, and even the experience of the modeling group (Pielke and Conant 2003). Engaging risk analysts and communicators who understand decisionmaking under uncertainty and who use maps in other fields (e.g., human and animal health) may help to define effective ways of communicating risk through maps.

6. Work toward pest risk maps that include impacts. Most pest risk maps report risk as the relative likelihood of a species' entry or establishment, without addressing potential impacts in those areas, such as yield loss or environmental damage over a forecast horizon. Some models have reported the number of generations or infection cycles that a pest may complete in a certain climate, and these measures have been used as an indicator of potential damage. The development of pest risk maps that include impacts will require a multidisciplinary approach and will especially involve greater cooperation with economists, ecologists, social scientists, and decisionmakers.

7. Increase international collaboration. International collaboration is key for the future development of pest risk modeling tools. International involvement will ensure that the widest possible talent pool is brought to bear in solving emerging problems, and will help to ensure modeling tools enjoy widespread acceptance. Such cooperation might be encouraged through regular workshops and the sharing of information resources. However, collaborators should be aware of the potential political and economic implications of some information, especially distribution records for certain pests. The presence of certain pests may provide adequate justification for other countries to deny commodities or conveyances from an infested country. The economic consequences of these restrictions could be significant.

8. Incorporate climate change. Climate change poses a set of challenges for the development and interpretation of pest risk maps. As the climate changes, so do species' distributions (Parmesan et al. 1999). The geographic ranges of relatively sessile species may be lagging behind their optimal climatic envelope, creating a technical problem for modeling their potential ranges. For temperate species, as temperatures rise, individuals and populations at the warmer edge of the present range are likely to become restricted to favorable microhabitats before they go locally extinct. On the cooler edge of the range, competition with resident species is likely to intensify and induce lags as species attempt to move to occupy new territories that are becoming more climatically suitable. Most ecological niche models assume that species ranges are in equilibrium with their environments. Because many climate-based habitat models use the so-called reference climate (1961–1990 average monthly normals), as climates warm and species distributions change, the relationship between the species' known range and the reference climate is likely to diverge. One partial

solution is to update the climate databases used for model calibration (Baker et al. 2000), though this approach may be confounded by lags in species range shifts.

A remaining challenge is to match the species' known range with the relevant climate. Myriad general circulation models exist and new models are being developed to project future climate conditions. Output data from these models can be downscaled and entered into pest risk models. For example, Baker and colleagues (2000) used CLIMEX to infer parameters describing climatic requirements and tolerances for the Colorado potato beetle, *Leptinotarsa decemlineata*. They then applied this model to downscaled output from the general circulation model HadCM2 (Hadley Centre, Exeter, United Kingdom) and were able to project increases in the Ecoclimatic Index, a measure of year-round climate suitability, in much of Europe by 2050 (figure 6). Pest risk analysts should proceed cautiously and attempt to explicitly account for the additional uncertainty that comes with long-term climate projections in descriptions of uncertainty with a pest risk model and associated map.

Pest risk models with a climate-change component provide an opportunity to test hypotheses and reexamine some macroecological assumptions that may have become entrenched in invasion ecology and species-distribution modeling literature. For example, such studies should help define over what time or spatial scale a species' range could be considered stable enough to fulfill assumptions about equilibrium in population or evolutionary models (Holt et al. 2005), and the relative importance of variation in environmental conditions, plastic responses, species interactions, range edges, and anthropogenic impacts on species' range changes (e.g., Sagarin et al. 2006).

9. Study how human and biological dimensions interact. Most of the risk maps that have been developed to date focus on biological dimensions of the risk problem; for example, the influence of climate on pest or host development. Human elements of the risk equation have received relatively little attention, with the exception of the human role in pest arrival. Human modifications to ecosystems through crop irrigation, crop protection, or urban development may increase or diminish the probability of establishment, depending on the species. Forest fragmentation, for example, may create edges that can be readily colonized by many invasive plants. Human activities such as domestic trade and transportation introduce stochasticity into patterns and rates of spread. Better theoretical models are needed to describe human-mediated movements of species through human-modified landscapes.

10. Provide training in pest risk modeling practice. The number of pest risk map users continues to increase. There are currently no regular formal training programs that explore the application and development of pest risk models and maps. Distributors of some model packages (e.g., CLIMEX) already provide ad hoc training classes, whereas other packages (e.g., NAPPFAST) are used only by a relatively small

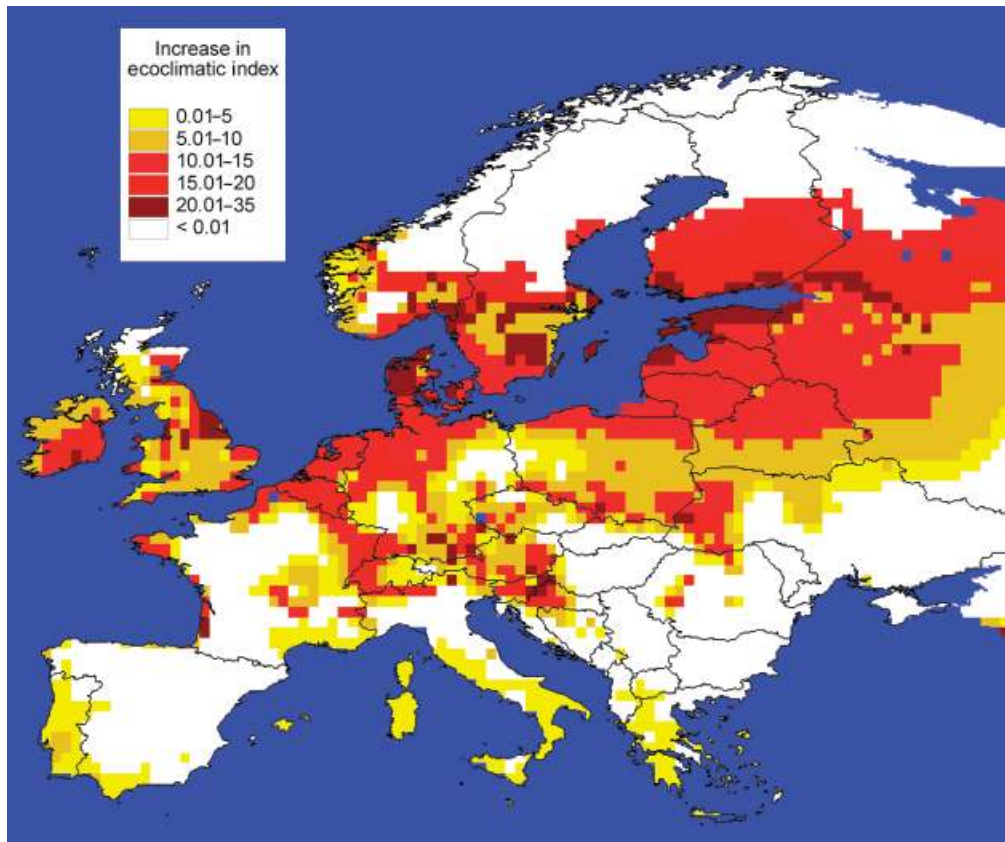


Figure 6. Projected increases in climatic suitability for *Leptinotarsa decemlineata*, the Colorado potato beetle, in Europe by 2050 based on a projected future climate scenario from the general circulation model, HadCM2. Climatic suitability was measured by the Ecoclimatic Index from CLIMEX, and the increases represent deviations from model results based on 1961–1990 climate normals. Map reprinted from Baker and colleagues (2000) with permission of Elsevier.

group of users who know the technology well and need little training. Training is critically important to ensure analysts understand the strengths and weaknesses of the approaches they are using to create pest risk models.

Conclusions

Pest risk maps graphically illustrate where an alien species might invade and have undesirable impacts. The quality of the map is subject to the constraints of available knowledge about the biology of the species and the environmental conditions within an area of interest, and the map's quality should be considered when making decisions. Certainly, one approach to improving pest risk maps is to gather more biological or geographic information (e.g., Kriticos et al. 2007). This approach is laudable, but decisionmakers are often politically and legislatively required to make decisions using available information and cannot wait for new research results.

A complete pest risk assessment blends the results of a pest risk map with expert judgments to provide information for decisionmakers. To date, national plant and animal health protection organizations have been the primary users

of pest risk maps. Greater demands for more strategic responses to invasive alien species are driving many organizations to develop and use their own pest risk maps. For an effective transfer of knowledge, pest risk analysts should provide greater detail about how their models were developed and evaluated than they currently do. How to communicate this information most effectively is still being debated.

Pest risk models and maps can play pivotal roles in the study of invasive alien species. Initial pest risk models can inform specific hypotheses for controlled experiments or observational studies, the results of which should stimulate reevaluation of the original risk models and risk maps. To achieve this dynamic feedback and abate confusion about future revisions to a map, communication about the extent and causes of

uncertainty associated with any risk map is critical. Fear of possible confusion or miscommunication should not be used as rationale for strict adherence to an initial risk map, especially if future versions are demonstrably better. In addition, researchers should be encouraged to perform meta-analyses of previous assessments to reveal consistent strengths or weaknesses of particular pest risk models. Only by better understanding the strengths and weaknesses of our current approaches can we hope to make significant improvements in pest risk maps and resulting risk-management decisions.

Future pest risk maps must address more elements of invasion risk than simply where an invasive alien species might establish. More rigorous analyses of historical and projected trade patterns, for example, are needed to better estimate where invasive alien pests might originate or first arrive (Richardson and Thuiller 2007). Analyses of synoptic weather events, for instance, might refine projected patterns of spread. Myriad tools are needed to better project the impacts of invasive alien species. Although ecological niche models are useful instruments to describe patterns in pest establishment, they do not reflect all of the factors that affect pest risk.

The group of scientists who developed the recommendations above will endeavour to tackle some of these challenges. We recognize the interdisciplinary nature of the problems that we face. Without assistance from trade analysts, meteorologists, economists, and social scientists, among others, many of these issues are likely to go unresolved. We welcome their contributions to help resolve these issues.

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References cited

- Andrewartha HG, Birch LC. 1954. *The Distribution and Abundance of Animals*. University of Chicago Press.
- Araújo MB, New M. 2007. Ensemble forecasting of species distributions. *Trends in Ecology and Evolution* 22: 42–47.
- Austin MP, Meyers JA. 1996. Current approaches to modelling the environmental niche of eucalypts: Implications for management of forest biodiversity. *Forest Ecology and Management* 85: 95–106.
- Baker RHA. 2002. Predicting the limits to the potential distribution of alien crop pests. Pages 207–241 in Hallman GJ, Schwalbe CP, eds. *Invasive Arthropods in Agriculture*. Science Publishers.
- Baker RHA, Sansford CE, Jarvis CH, Cannon RJC, MacLeod A, Walters KFA. 2000. The role of climatic mapping in predicting the potential geographic distribution of non-indigenous pests under current and future climates. *Agriculture, Ecosystems and Environment* 82: 57–71.
- Barry S, Elith J. 2006. Error and uncertainty in habitat models. *Journal of Applied Ecology* 43: 413–423.
- Bates JM, Granger CWJ. 1969. The combination of forecasts. *Operational Research Quarterly* 20: 451–468.
- Beale CM, Lennon JJ, Gimona A. 2008. Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences* 105: 14908–14912.
- Brown JH, Stevens GC, Kaufman DM. 1996. The geographic range: Size shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* 27: 597–623.
- Buizza R, Houtekamer PL, Toth Z, Pellerin G, Wei M, Zhu Y. 2005. A comparison of the ECMWF, MSC and NCEP global ensemble prediction systems. *Monthly Weather Review* 133: 1076–1097.
- Bulmer M. 2005. The theory of natural selection of Alfred Russel Wallace FRS. *Notes and Records of the Royal Society* 59: 125–136.
- Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391: 783–786.
- Elith J, Burgman MA, Regan HM. 2002. Mapping epistemic uncertainties and vague concepts in predictions of species distribution. *Ecological Modelling* 157: 313–329.
- Elith J, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151.
- [FAO] Food and Agriculture Organization. 2007. *International Standards for Phytosanitary Measures (ISPM No. 2): Framework for Pest Risk Analysis*. Secretariat of the International Plant Protection Convention.
- Fielding AH, Bell JE. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38–49.
- Gevrey M, Worner SP. 2006. Prediction of global distribution of insect pest species in relation to climate by using an ecological informatics method. *Journal of Economic Entomology* 99: 979–986.
- Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186.
- Hartley S, Harris R, Lester PJ. 2006. Quantifying uncertainty in the potential distribution of an invasive species: Climate and the Argentine ant. *Ecology Letters* 9: 1068–1079.
- Harvey PH, Colwell RK, Silvertown JW, May RM. 1983. Null models in ecology. *Annual Review of Ecology and Systematics* 14: 189–211.
- Hirzel AH, Le Lay G. 2008. Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45: 1372–1381.
- Hodkinson ID. 1999. Species response to global environmental change or why ecophysiological models are important: A reply to Davis et al. *Journal of Animal Ecology* 68: 1259–1262.
- Holt RD, Keitt TH, Lewis MA, Maurer BA, Taper ML. 2005. Theoretical models of species' borders: Single species approaches. *Oikos* 108: 18–27.
- Hutchinson RE. 1957. Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* 22: 415–427.
- Isard SA, Russo JM, DeWolf ED. 2006. The establishment of a national pest information platform for extension and education. *Plant Health Progress*. doi:1094/PHP-2006-0915-01-RV
- Jarvis CH, Baker RHA. 2001. Risk assessment for nonindigenous pests: 1. Mapping the outputs of phenology models to assess the likelihood of establishment. *Diversity and Distributions* 7: 223–235.
- Jeffers JNR. 1988. *Ecological systems and their dynamics*. Pages 5–57 in Jeffers JNR, ed. *Practitioner's Handbook on the Modelling of Dynamic Change in Ecosystems*. Wiley.
- Johnson CJ, Gillingham MP. 2004. Mapping uncertainty: Sensitivity of wildlife habitat ratings to expert opinion. *Journal of Applied Ecology* 41: 1032–1041.
- Kriticos DJ, Randall RP. 2001. A comparison of systems to analyze potential weed distributions. Pages 61–79 in Groves RH, Panetta FD, Virtue JG, eds. *Weed Risk Assessment*. CSIRO.
- Kriticos DJ, Potter KJB, Alexander NS, Gibb AR, Suckling DM. 2007. Using a pheromone lure survey to establish the native and potential distribution of an invasive Lepidopteran, *Uraba lugens*. *Journal of Applied Ecology* 44: 853–863.
- Lobo JM, Jiménez Valverde A, Real R. 2008. AUC: A misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17: 145–151.
- MacArthur RH. 1960. Review of 'Population studies: Animal ecology and demography.' *Quarterly Review of Biology* 35: 82–83.
- Magarey RD, Fowler GA, Borchert DM, Sutton TB, Colunga-Garcia M, Simpson JA. 2007. NAPPFAST: An Internet system for the weather-based mapping of plant pathogens. *Plant Disease* 91: 336–345.
- McKenney DW, Pedlar JH, Lawrence K, Campbell K, Hutchinson ME. 2007. Beyond traditional hardness zones: Using climate envelopes to map plant range limits. *BioScience* 57: 929–937.
- Monmonier M. 1996. *How to Lie with Maps*. University of Chicago Press.
- Nicholson AJ. 1954. An outline of the dynamics of animal populations. *Australian Journal of Zoology* 2: 9–65.
- Nix HA. 1986. A biogeographic analysis of Australian elapid snakes. Pages 4–15 in Longmore R, ed. *Atlas of Elapid Snakes of Australia*. Australian Government Printing Service.
- Parmesan C, et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579–583.

- Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, Miles L, Segurado P, Dawson TP, Lees DC. 2006. Model-based uncertainty in species range prediction. *Journal of Biogeography* 33: 1704–1711.
- Peterson AT, Vieglais DA. 2001. Predicting species invasions using ecological niche modeling: New approaches from bioinformatics attack a pressing problem. *BioScience* 51: 363–371.
- Peterson AT, Papes M, Soberon J. 2008. Rethinking receiver operator characteristic analysis applications in ecological niche modeling. *Ecological Modelling* 213: 63–72.
- Phillips SJ. 2008. Transferability, sample selection bias and background data in presence-only modelling: A response to Peterson et al. (2007). *Ecography* 31: 272–278.
- Pielke RA, Conant RT. 2003. Best practices in prediction for decision-making: Lessons from the atmospheric and earth sciences. *Ecology* 84: 1351–1358.
- Pitt JPW, Worner SP, Suarez AV. 2009. Predicting Argentine ant spread over the heterogeneous landscape using a spatially explicit stochastic model. *Ecological Applications* 19: 1176–1186.
- Regan HM, Colyvan M, Burgman MA. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecological Applications* 12: 618–628.
- Regan HM, Akçakaya HR, Ferson S, Root KV, Carroll S, Ginzburg LR. 2003. Treatments of uncertainty and variability in ecological risk assessment of single-species populations. *Human and Ecological Risk Assessment* 9: 889–906.
- Richardson DM, Thuiller W. 2007. Home away from home—objective mapping of high-risk source areas for plant introductions. *Diversity and Distributions* 13: 299–312.
- Sagarin RD, Gaines SD, Gaylord B. 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology and Evolution* 21: 524–530.
- Sheehan KA. 1992. User's Guide for GMPHEN: Gypsy Moth Phenology Model. United States Department of Agriculture, Forest Service. General Technical Report NE-158.
- Shelford VE. 1963. *The Ecology of North America*. University of Illinois Press.
- Stockwell D. 2006. *Niche Modeling: Predictions from Statistical Distributions*. Chapman and Hall/CRC.
- Sutherst RW, Bourne AS. 2009. Modelling non-equilibrium distributions of invasive species: A tale of two modelling paradigms. *Biological Invasions* 11: 1231–1237.
- Sutherst RW, Maywald GF. 1985. A computerised system for matching climates in ecology. *Agriculture, Ecosystems and Environment* 13: 281–299.
- Sutherst RW, Maywald GF, Skarratt RB. 1995. Predicting insect distributions in a changed climate. Pages 59–91 in Harrington R, Stork NE, eds. *Insects in a Changing Environment*. Academic Press.
- [USDA] United States Department of Agriculture. 2004. *Sudden Oak Death: Protecting America's Woodlands from *Phytophthora ramorum**. State and Private Forestry, USDA Forest Service. Publication no. FS-794.
- Usio N, Nakajima H, Kamiyama R, Wakana I, Hiruta S, Takamura N. 2006. Predicting the distribution of invasive crayfish (*Pacifastacus leniusculus*) in a Kusiro Moor marsh (Japan) using classification and regression trees. *Ecological Research* 21: 271–277.
- van der Ploeg RR, Böhm W, Kirkham MB. 1999. On the origin of the theory of mineral nutrition of plants and the law of the minimum. *Soil Science Society of America Journal* 63: 1055–1062.
- Venette RC, Cohen SD. 2006. Potential climatic suitability for establishment of *Phytophthora ramorum* in the contiguous United States. *Forest Ecology and Management* 231: 18–26.
- Venette RC, Koch RL. 2009. IPM for invasive species. Pages 424–436 in Radcliffe EB, Hutchison WD, Cancelado RE, eds. *Integrated Pest Management: Concepts, Tactics, Strategies, and Case Studies*. Cambridge University Press.
- Venette RC, Moon RD, Hutchison WD. 2002. Strategies and statistics of sampling for rare individuals. *Annual Review of Entomology* 47: 143–174.
- Woodbury PB. 2003. Dos and don'ts of spatially explicit ecological risk assessments. *Environmental Toxicology and Chemistry* 22: 977–982.
- Worner SP. 2002. Predicting the invasive potential of exotic insects. Pages 119–137 in Hallman GJ, Schwalbe CP, eds. *Invasive Arthropods in Agriculture*. Science Publishers.
- Yemshanov D, Koch FH, McKenney DW, Downing MC, Sapio F. 2009. Mapping invasive species risks with stochastic models: A cross-border United States-Canada application for *Sirex noctilio* Fabricius. *Risk Analysis* 29: 868–884.

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