

Advancing risk assessment models to address climate change, economics and uncertainty

Edited by

Darren J. Kriticos and Robert C. Venette



Sofia–Moscow

2013

NEOBIOTA 18 (SPECIAL ISSUE)

ADVANCING RISK ASSESSMENT MODELS TO ADDRESS CLIMATE CHANGE, ECONOMICS AND UNCERTAINTY

Edited by Darren J. Kriticos and Robert C. Venette

A collection of papers presented at the OECD Co-operative Research Programme-sponsored workshop held during the VIth meeting of the International Pest Risk Mapping Workgroup, 23-26 July 2012, Tromsø, Norway.

The opinions expressed and arguments employed in this publication are the sole responsibility of the authors and do not necessarily reflect those of the OECD or of the governments of its Member countries.

Front cover image used with permission.

Credit: Tom Hlavaty, USDA Agricultural Research Service, Bugwood.org.

The workshop was sponsored by the OECD Co-operative Research Programme on Biological Resource Management for Sustainable Agricultural Systems, whose financial support made it possible for most of the invited speakers to participate in the Workshop



First published 2013

ISBN 978-954-642-699-4 (paperback)

Pensoft Publishers

12 Prof. Georgi Zlatarski Street, 1700 Sofia, Bulgaria

Fax: +359-2-870-42-82

info@pensoft.net

www.pensoft.net

Printed in Bulgaria, September 2013

Contents

- 1 **Invasive alien species in the food chain: Advancing risk assessment models to address climate change, economics and uncertainty**
Darren J. Kriticos, Robert C. Venette, Richard H.A. Baker, Sarah Brunel, Frank H. Koch, Trond Rafoss, Wopke van der Werf, Susan P. Worner
- 9 **Interface between pest risk science and policy: the EPPO perspective**
Sarah Brunel, Muriel Suffert, Françoise Petter, Richard Baker
- 25 **Matching methods to produce maps for pest risk analysis to resources**
Richard H.A. Baker, Dominic Eyre, Sarah Brunel
- 41 **Practical guidelines for modelling post-entry spread in invasion ecology**
Hazel R. Parry, Rohan J. Sadler, Darren J. Kriticos
- 67 **An assessment of the benefits of yellow Sigatoka (*Mycosphaerella musicola*) control in the Queensland Northern Banana Pest Quarantine Area**
David C. Cook, Shuang Liu, Jacqueline Edwards, Oscar N. Villalba, Jean-Philippe Aurambout, Darren J. Kriticos, Andre Drenth, Paul J. De Barro
- 83 **Prioritizing the risk of plant pests by clustering methods; self-organising maps, k-means and hierarchical clustering**
Susan P. Worner, Muriel Gevrey, René Eschen, Marc Kenis, Dean Paini, Sunil Singh, Karl Suiter, Michael J. Watts
- 103 **Understanding trade pathways to target biosecurity surveillance**
Manuel Colunga-Garcia, Robert A. Haack, Roger D. Magarey, Daniel M. Borchert
- 119 **Improving pest risk assessment and management through the aid of geospatial information technology standards**
Trond Rafoss, Jarle Skahjem, John Atle Johansen, Ståle Johannessen, Udaya Sekhar Nagothu, Inger S. Fløistad, Arild Sletten
- 131 **Incorporating climate change into pest risk models for forest pathogens: a role for cold stress in an era of global warming?**
Robert C. Venette
- 151 **Could natural selection change the geographic range limits of light brown apple moth (Lepidoptera, Tortricidae) in North America?**
Amy C. Morey, Robert C. Venette, William D. Hutchison

- 157 Uncertainty and sensitivity analysis in quantitative pest risk assessments; practical rules for risk assessors**
David Makowski
- 173 Representing uncertainty in a spatial invasion model that incorporates human-mediated dispersal**
Frank H. Koch, Denys Yemshanov, Robert A. Haack
- 193 Quantifying uncertainty in pest risk maps and assessments: adopting a risk-averse decision maker's perspective**
Denys Yemshanov, Frank H. Koch, Mark J. Ducey, Robert A. Haack, Marty Siltanen, Kirsty Wilson

Invasive alien species in the food chain: Advancing risk assessment models to address climate change, economics and uncertainty

Darren J. Kriticos¹, Robert C. Venette², Richard H.A. Baker³, Sarah Brunel⁴, Frank H. Koch⁵, Trond Rafoss⁶, Wopke van der Werf⁷, Susan P. Worner⁸

1 CSIRO Ecosystem Sciences and Biosecurity Flagship, GPO Box 1700, Canberra, ACT 2601, Australia
2 USDA Forest Service, Northern Research Station, St. Paul, MN 55108 USA **3** The Food and Environment Research Agency, Sand Hutton, York YO41 1LZ, UK **4** European and Mediterranean Plant Protection Organization (EPPO/OEPP), 21 boulevard Richard Lenoir 75011, Paris, France **5** USDA Forest Service, Southern Research Station, Eastern Forest Environmental Threat Assessment Center, 3041 Cornwallis Road, Research Triangle Park, NC 27709 USA **6** Bioforsk – Norwegian Institute for Environmental and Agricultural Research, Høgskoleveien 7, 1342 Ås, Norway **7** Wageningen University, Plant Sciences, Centre for Crop Systems Analysis, Crop & Weed Ecology Group, P.O. Box 430, 6700 AK Wageningen, The Netherlands **8** Bio-Protection Research Centre, PO Box 84, Lincoln University, Lincoln 7647 New Zealand.

Corresponding author: Darren Kriticos (darren.kriticos@csiro.au)

Received 18 August 2013 | Accepted 21 August 2013 | Published 13 September 2013

Citation: Kriticos DJ, Venette RC, Baker RHA, Brunel S, Koch FH, Rafoss T, van der Werf W, Worner SP (2013) Invasive alien species in the food chain: Advancing risk assessment models to address climate change, economics and uncertainty. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 1–7. doi: 10.3897/neobiota.18.6108

Economic globalization depends on the movement of people and goods between countries. As these exchanges increase, so does the potential for translocation of harmful pests, weeds, and pathogens capable of impacting our crops, livestock and natural resources (Hulme 2009), with concomitant impacts on global food security (Cook et al. 2011).

Potential invasions by alien species create a dilemma for nations that engage in international trade. On one hand, free trade may provide new markets for producers, cheaper and more diverse goods for consumers, and increase overall gross domestic product. On the other hand, unfettered trade may allow new pests to arrive and jeopardize domestic agricultural industries. Pests may lower agricultural production, reduce the marketability of a crop, or trigger quarantine restrictions from other coun-

tries to prevent the continued spread of the pest. The challenge, then, is to identify the risks associated with particular organisms, commodities, or pathways and mitigate those risks to desirable levels. Pest risk assessment, the process by which scientific evidence is used to assess the likelihood that a pest might invade and the extent of harm should the invasion be successful, is commonly applied to decide whether to engage in agricultural trade with another nation and whether phytosanitary precautions might be required in order to manage the risks (Magarey et al. 2009, Schrader et al. 2010). When conducted properly, risk assessments can avert economic losses and preserve economic activity (Keller et al. 2007).

Pest risk maps illustrate where invasive alien arthropods, molluscs, pathogens, and weeds might become established, spread, and cause harm to natural and agricultural resources within a pest risk area. Such maps can be powerful tools to assist policymakers in matters of international trade, domestic quarantines, biosecurity surveillance, or pest-incursion responses. The International Pest Risk Mapping Workgroup (IPRMW) is a group of ecologists, economists, modellers, and practising risk analysts who are committed to improving the methods used to estimate risks posed by invasive alien species to agricultural and natural resources. The group also strives to improve communication about pest risks to biosecurity, production, and natural-resource-sector stakeholders so that risks can be better managed. The IPRMW previously identified ten activities to improve pest risk assessment procedures, among these were: “improve representations of uncertainty, … expand communications with decision-makers on the interpretation and use of risk maps, … increase international collaboration, … incorporate climate change, … [and] study how human and biological dimensions interact” (Venette et al. 2010).

The IPRMW met in Tromsø, Norway from 23–26 July, 2012 to address the specific challenges of incorporating climate change into long-term risk projections for invasive alien species, estimating the economic effects of species invasions, and incorporating uncertainty in risk models. A special symposium focused on the interface between pest risk science and policy. The meeting was attended by 30 ecologists, economists, risk analysts and policy advisors from Australia, New Zealand, Canada, the United Kingdom, Finland, Norway, the Netherlands, Hungary, France, Italy, and the United States. The conference succeeded in stimulating new ideas about how to incorporate climate change, invasion dynamics, economics, and uncertainty into pest risk models and maps for invasive alien species, and how to communicate these improved results to biosecurity policy advisors. This special issue of NeoBiota documents the proceedings of the meeting, and this overview summarizes major findings.

Pest risk science and policy. Effective management of biosecurity risks requires close interactions between pest risk assessors and risk managers. Risk assessors evaluate the probability and magnitude of harm from new species incursions and may evaluate options to mitigate those risks. Risk managers within national biosecurity agencies and regional plant protection organizations may draw upon scientific and modelling inputs as they develop standards and implementation plans for phytosanitary measures and other biosecurity procedures. Pest risk assessment methods being developed

or enhanced by this workgroup frequently underpin decisions about which species to survey and regulate. For example, the European and Mediterranean Plant Protection Organisation (EPPO) has adopted the risk assessment framework developed under the IPRMW-affiliated PRATIQUE project (Brunel et al. 2013). Economics offers policy analysis tools that estimate the likely impacts an invasive species might have on an economy under a range of policy scenarios. They can analyse these threats from a range of social, environmental and economic perspectives to help guide policymakers to assess what, if anything, should be done to mitigate or ameliorate these threats. Practical constraints (e.g., information quality and quantity) and procedural constraints (e.g., public comment periods) can affect risk assessors' choices about which methods to use to develop pest risk maps. The challenge for pest risk modellers is to try to balance rigor and timeliness in their work to obtain degrees of accuracy and precision that are acceptable to policy advisors and to help policy advisors understand the meaning of their work. For policy advisors, the challenge is to articulate clearly what information is needed to support time-critical decision-making.

Pest risk and climate change. Climate change is expected to affect the distribution and phenology of pests and crops. Some invasive alien species may pose threats to more poleward and higher-altitude regions as cold-related range limits are relaxed. For example, the citrus longhorn beetle, *Anoplophora chinensis* (Forster), is present in southern Europe (Caremi and Ciampitti 2006), but is only reported as transient under eradication in Denmark and the United Kingdom (EPPO 2013). It appears that *A. chinensis* could cause significant damage in parks, gardens, and forests in some coastal areas of northern Europe if it is able to overwinter there in the future. Models have identified other, currently-damaging species situations that may become less problematic as future heat-stress increases. For migratory pests such as aphids, climate change may alter the spatio-temporal synchronization of the pest and crop, affecting the extent of damage such pests may cause. Furthermore, elevated levels of atmospheric carbon dioxide are likely to stimulate plant growth in many crops, perhaps offsetting some damage from invasive alien species. Studies are being conducted to quantify the rate at which natural selection drives adaptation to local conditions in an invading species (Morey et al. 2013). The outcomes of this work will provide a better understanding of the reliability of niche models for describing species' potential ranges in novel environments. The effects of projected climate changes on pest risk models are being investigated by applying global climate scenarios to species niche models (Venette 2013). Given significant uncertainties about climate change and subsequent biological responses, adaptive management methods, guided by models, seem prudent to address future risks from invasive alien species. An adaptive management method balances the desire to avoid unwarranted expenditure on preventing or ameliorating risks that may not arise, whilst identifying adaptive measures that may be necessary if evidence indicates that the risks are likely to emerge in the near future.

Pest risk and economics. Economic analysis tools such as benefit-cost analysis and break-even analysis are effective in condensing complex information into relatively simple metrics about the potential impacts from invasive alien species and the poten-

tial benefits of preventative or ameliorative actions. These tools are particularly useful when the impacts of invasive species are limited to agricultural commodities because of the relative ease with which impacts can be quantified. Economic pest impact models are increasingly taking discounting effects into account by considering the rate of spread of pests. Whilst spread models can inform where invasive species might occur (at least in the short-term) (Robinet et al. 2012; Parry et al. 2013), their most important contribution to economics may be to simply estimate the rate of spread of pests through time. Methods that integrate simple pest spread and climate suitability models with crop productivity models have been developed to estimate economic aspects of pest risk in terms that are compatible with the International Standards for Phytosanitary Measures (Cook et al. 2013; Kriticos et al. 2013).

Pest invasions, spread, and surveillance. Biosecurity policies and procedures are frequently intended to prevent the introduction, or slow the spread, of invasive alien species. A significant gap remains between what we know and what we need to know about invasion pathways, especially those related to human activities. Probabilistic pathway models that link the arrival of invasive organisms to existing international and domestic trade flows and transportation corridors are being developed to estimate rates of pest arrivals at specific locations (Colunga-Garcia et al. 2013).

Risk-scoring methods exist to help prioritize species, often only requiring coarse characterizations of species traits. These methods are popular amongst biosecurity agencies, although doubts remain about their subjectivity and accuracy (Caley et al. 2008). A new method analyses the geographical distribution of species assemblages objectively to estimate the relative potential of new species to become established should they be introduced to an area of concern (Worner et al. 2013). New geospatial data standards allow synthesis of diverse geographical data to improve pest detections in the field (Rafoss et al. 2013). New statistical treatments of survey data evaluate biosecurity strategies more rigorously, particularly when detection surveys fail to find a targeted pest.

Even under the best of circumstances, pest risk maps are often challenging to develop and difficult to interpret correctly. Decision support systems are being developed to address these issues, ensuring that pest risk maps are fit for purpose and contribute fully to plant health biosecurity (Baker et al. 2012; Baker et al. 2013).

Pest risk and uncertainty. Uncertainty in risk estimates arises from a number of sources. If policymakers fail to consider uncertainty, they may make unwise decisions. Uncertainty can arise from a fundamental lack of knowledge of risk elements. This epistemic uncertainty can impact decisions such as which species to target during biosecurity surveillance, or whether it is better to apply resources to preventative measures at the expense of surveillance. Another source of uncertainty is inherent variation in risk components. New analytical methods are being developed to provide formal quantitative treatments of parametric uncertainty (Makowski 2013) and to address the perceived risk aversion of some biosecurity decision-makers (Yemshanov et al. 2013). Initial investigations suggest that the incorporation of a policy maker's risk perceptions adds credibility to pest risk maps, and narrows the set of geographical locations that

would need to be targeted by costly inspections and public outreach activities. Methods for representing the uncertainty in spatial invasion models were demonstrated using a case study involving human-mediated dispersal of invasive forest pests in camper-transported firewood (Koch et al. 2013). This analysis was then extended to include consideration of the relative risk-aversion of decision makers who rely on risk model outputs for guidance.

Since its first meeting in 2007, the IPRMW has made significant advances in pest risk modelling and mapping methods. The meeting in Tromsø continued this tradition, with significant advances in economic model integration, a new understanding of the irreducible uncertainties in climate change forecasts and the desirability of an adaptive management framework for dealing with these uncertainties, as well as new methods for dealing with other forms of uncertainty. Clearly, more work needs to be done in the area of risk communication and the improvement of niche modelling methods to produce timely and reliable models.

Acknowledgements

We would like to thank the Co-operative Research Programme on Biological Resource Management for Sustainable Agricultural Systems (CRP) of the Organisation for Economic Co-operation and Development for sponsoring the sixth meeting of the International Pest Risk Mapping Workgroup. We especially thank Janet Schofield for her assistance in organizing the meeting, and OECD-CRP representatives Carl-Christian Schmidt, Gary Fitt, and Wayne Martindale for their participation in the meeting. We thank Bioforsk – the Norwegian Institute for Agricultural and Environmental Research – for hosting the conference and Øystein Ballari, Kari Munthe, Arne Hermansen and Erling Fløistad for their assistance with local arrangements. We thank Manuel Colunga-Garcia, David Cook, Martin Damus, Elizabeth Daugharty, Paul De Barro, Mark Ducey, Bob Douma, Dominic Eyre, Jaakko Heikkilä, Arne Hermansen, Tom Kalaris, Christer Magnuson, Amy Morey, Hazel Parry, Daniel de Rigo, Leif Sundheim, Karl Suiter, Mark Szalai and Denys Yemshanov for engaging presentations and thoughtful conversations during the conference. Lastly, we thank Roger Magarey for serving as an academic editor during the production of these proceedings.

References

- Baker RHA, Benninga J, Bremmer J, Brunel S, Dupin M, Eyre D, Ilieva Z, Jarošík V, Kehlenbeck H, Kriticos DJ, Makowski D, Pergl J, Reynaud P, Robinet C, Soliman T, Van der Werf W, Worner SP (2012) A decision support scheme for mapping endangered areas in pest risk analysis. EPPO Bulletin 42: 65–73.
- Baker RHA, Eyre D, Brunel S (2013) Matching methods to produce maps for pest risk analysis to resources. In: Kriticos DJ, Venette RC (Eds) *Advancing risk assessment models to*

- address climate change, economics and uncertainty. *NeoBiota* 18: 25–40. doi: 10.3897/neobiota.18.4056
- Brunel S, Suffert M, Petter F, Baker R (2013) Interface between pest risk science and policy: the EPPO perspective. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models of invasive alien species in the food chain. *NeoBiota* 18: 9–23. doi: 10.3897/neobiota.18.4049
- Caley P, Groves RH, Barker R (2008) Estimating the invasion success of introduced plants. *Diversity and Distributions* 14: 196–203.
- Caremi G, Ciampitti M (2006) Il coleottero *Anoplophora chinensis* in Lombardia: diffusione e strategie di controllo. *Atti Giornate Fitopatologiche I*: 205–210.
- Colunga-Garcia M, Haack RA, Magarey RD, Borchert DM (2013) Understanding trade pathways to target biosecurity surveillance. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. *NeoBiota* 18: 103–118. doi: 10.3897/neobiota.18.4019
- Cook DC, Fraser RW, Paini DR, Warden AC, Lonsdale WM, De Barro PJ (2011) Biosecurity and yield improvement technologies are strategic complements in the fight against food insecurity. *PLoS One* 6: e26084. doi: 10.1371/journal.pone.0026084
- Cook DC, Liu S, Edwards J, Villalta ON, Aurambout J-P, Kriticos DJ, Drenth A, De Barro PJ (2013) An assessment of the benefits of yellow Sigatoka (*Mycosphaerella musicola*) control in the Queensland Northern Banana Pest Quarantine Area. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. *NeoBiota* 18: 67–81. doi: 10.3897/neobiota.18.3863
- EPPO (2013) PQR - EPPO database on quarantine pests (available online). www.eppo.int/DATABASES/pqr/pqr.htm
- Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18. doi: 10.1111/j.1365-2664.2008.01600.x
- Keller RP, Lodge DM, Finnoff DC (2007) Risk assessment for invasive species produces net bioeconomic benefits. *Proceedings of the National Academy of Sciences of the United States of America* 104: 203–207. doi: 10.1073/pnas.0605787104
- Koch FH, Yemshanov D, Haack RA (2013) Representing uncertainty in a spatial invasion model that incorporates human-mediated dispersal. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. *NeoBiota* 18: 173–191. doi: 10.3897/neobiota.18.4016
- Kriticos DJ, Leriche A, Palmer D, Cook DC, Brockerhoff EG, Stephens AEA, Watt MS (2013) Linking climate suitability, spread rates and host-impact when estimating the potential costs of invasive pests. *PLoS One* 8: e54861. doi: 10.1371/journal.pone.0054861
- Magarey RD, Colunga-Garcia M, Fieselmann DA (2009) Plant biosecurity in the United States: Roles, responsibilities, and information needs. *Bioscience* 59: 875–884.
- Makowski D (2013) Uncertainty and sensitivity analysis in quantitative pest risk assessments; practical rules for risk assessors. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. *NeoBiota* 18: 157–171. doi: 10.3897/neobiota.18.3993

- Morey AC, Venette RC, Hutchison WD (2013) Could natural selection change the geographic range limits of light brown apple moth (Lepidoptera, Tortricidae) in North America? In: Kriticos DJ, Venette RC (Eds) *Advancing risk assessment models to address climate change, economics and uncertainty*. NeoBiota 18: 151–156. doi: 10.3897/neobiota.18.5288
- Parry HR, Sadler RJ, Kriticos DJ (2013) Practical guidelines for modelling post-entry spread in invasion ecology. In: Kriticos DJ, Venette RC (Eds) *Advancing risk assessment models to address climate change, economics and uncertainty*. NeoBiota 18: 41–66. doi: 10.3897/neobiota.18.4305
- Rafoss T, Skahjem J, Johansen JA, Johannessen S, Nagothu US, Fløistad IS, Sletten A (2013) Improving pest risk assessment and management through the aid of geospatial information technology standards. In: Kriticos DJ, Venette RC (Eds) *Advancing risk assessment models to address climate change, economics and uncertainty*. NeoBiota 18: 119–130. doi: 10.3897/neobiota.18.4017
- Robinet C, Kehlenbeck H, Kriticos DJ, Baker RHA, Battisti A, Brunel S, Dupin M, Eyre D, Faccoli M, Ilieva Z, Kenis M, Knight J, Reynaud P, Yart A, van der Werf W (2012) A suite of models to support the quantitative assessment of spread in pest risk analysis. PLoS One 7: e43366. doi: 10.1371/journal.pone.0043366
- Schrader G, MacLeod A, Mittinty M, Brunel S, Kaminski K, Kehlenbeck H, Petter F, Baker R (2010) Enhancements of pest risk analysis techniques. Bulletin OEPP/EPPO Bulletin 40: 107–120. doi: 10.1111/j.1365-2338.2009.02360.x
- Venette RC (2013) Incorporating climate change into pest risk models for forest pathogens: a role for cold stress in an era of global warming? In: Kriticos DJ, Venette RC (Eds) *Advancing risk assessment models to address climate change, economics and uncertainty*. NeoBiota 18: 131–150. doi: 10.3897/neobiota.18.4047
- Venette RC, Kriticos DJ, Magarey R, Koch F, Baker RHA, Worner S, Gómez NN, McKenney D, Dobesberger E, Yemshanov D, De Barro P, Hutchison WD, Fowler G, Kalaris T, Pedlar J (2010) Pest risk maps for invasive alien species: a roadmap for improvement. Bioscience 80: 349–362.
- Worner SP, Gevrey M, Eschen R, Kenis M, Paini D, Singh S, Suiter K, Watts MJ (2013) Prioritizing the risk of plant pests by clustering methods; self-organising maps, k-means and hierarchical clustering. In: Kriticos DJ, Venette RC (Eds) *Advancing risk assessment models to address climate change, economics and uncertainty*. NeoBiota 18: 83–102. doi: 10.3897/neobiota.18.4042
- Yemshanov D, Frank FH, Ducey MJ, Haack RA, Siltanen M, Wilson K (2013) Quantifying uncertainty in pest risk maps and assessments: adopting a risk-averse decision maker's perspective. In: Kriticos DJ, Venette RC (Eds) *Advancing risk assessment models to address climate change, economics and uncertainty*. NeoBiota 18: 193–218. doi: 10.3897/neobiota.18.4002

Interface between pest risk science and policy: the EPPO perspective

Sarah Brunel¹, Muriel Suffert¹, Françoise Petter¹, Richard Baker²

1 European and Mediterranean Plant Protection Organization (EPPO/OEPP) - 21 boulevard Richard Lenoir 75011 PARIS- France **2** The Food and Environment Research Agency, Sand Hutton, York YO41 1LZ, UK

Corresponding author: Sarah Brunel (sb@eppo.int)

Academic editor: F. Koch | Received 26 September 2012 | Accepted 18 March 2013 | Published 13 September 2013

Citation: Brunel S, Suffert M, Petter F, Baker R (2013) Interface between pest risk science and policy: the EPPO perspective. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 9–23. doi: 10.3897/neobiota.18.4049

Abstract

The European and Mediterranean Plant Protection Organisation (EPPO) is an intergovernmental organization responsible for cooperation in plant protection in the European and Mediterranean region. It provides global distribution maps of pests, and intends to identify the areas at risk from new and emerging pests, in the framework of Pest Risk Analyses. EPPO has developed a decision-support scheme for Pest Risk Analysis (DSS) and a computer program (CAPRA) to assist pest risk analysts in running the decision-support scheme. Dedicated rating guidance and a Climatic Suitability Risk Mapping Decision-Support Scheme have recently been developed to guide assessors in identifying the potential area of establishment of a pest. All these tools have been developed taking into account both pest risk science available and needs of policy makers. The use of these tools and of mapping software are undertaken within the framework of EPPO Pest Risk Analyses, as illustrated through the examples of *Thaumatomibia leucotreta* (Lepidoptera) and *Apriona germari* (Coleoptera).

Keywords

Pest Risk Analysis, pest risk mapping, modelling, *Thaumatomibia leucotreta*, *Apriona germari*

Introduction

What is EPPO and what are EPPO pest risk mapping needs?

The European and Mediterranean Plant Protection Organization (EPPO) is the regional plant protection organization (RPPO) for Europe under the International Plant Protection Convention (IPPC). EPPO works with National Plant Protection Organizations (NPPOs) which are national bodies responsible for plant health policy. EPPO recommendations and Pest Risk Analyses (PRAs) may be used as basis for European Union or national regulations.

Founded in 1951, EPPO has grown from 15 original members to today's 50 member countries, including nearly every country in the European and Mediterranean region.

EPPO's objectives are to develop an international strategy against the introduction and spread of pests that damage cultivated and wild plants, in natural and agricultural ecosystems (including invasive alien plants); to encourage harmonization of phytosanitary regulations and all other areas of official plant protection action; to promote the use of modern, safe, and effective pest control methods; and to provide a documentation service on plant protection.

Such objectives are dealt with in part by providing regional maps on the distribution of pests, as well as by performing modelling to identify the probability of establishment of emerging pests in the EPPO region.

EPPO mapping: providing maps

EPPO maintains the Plant Quarantine data Retrieval system (PQR), which provides detailed information on the geographical distribution and host plants of quarantine pests and of pests of phytosanitary concern. For each pest, it is possible to obtain lists of host plants, commodities able to act as pathways in international trade, details of geographical distribution with maps, and pictures of the pest at different stages as well as of symptoms of the pest. Conversely, it is also possible to query the database to obtain specific lists of pests, by stipulating the host species, the commodity, and the countries of interest. PQR contains general nomenclatural and taxonomic details on pests and hosts. In recent years, the database has been extended to cover invasive alien plants, including those having environmental impacts. All EPPO activities and recommendations on invasive alien plants can be consulted on its dedicated webpages (see http://www.eppo.int/INVASIVE_PLANTS/ias_plants.htm). PQR is used by risk assessors to obtain accurate information on the distribution of pests. Inspectors also make use of PQR to select pests to look for in different consignments according to their origins. The new PQR version can be downloaded free of charge from the EPPO website and includes world maps (see http://www.eppo.int/DATABASES/pqr/pqr.htm?utm_source=www.eppo.org&utm_medium=int_redirect).

These world maps display the known distribution of pests covered by the EPPO framework (pests recommended for regulation, quarantine pests and pests in the EPPO

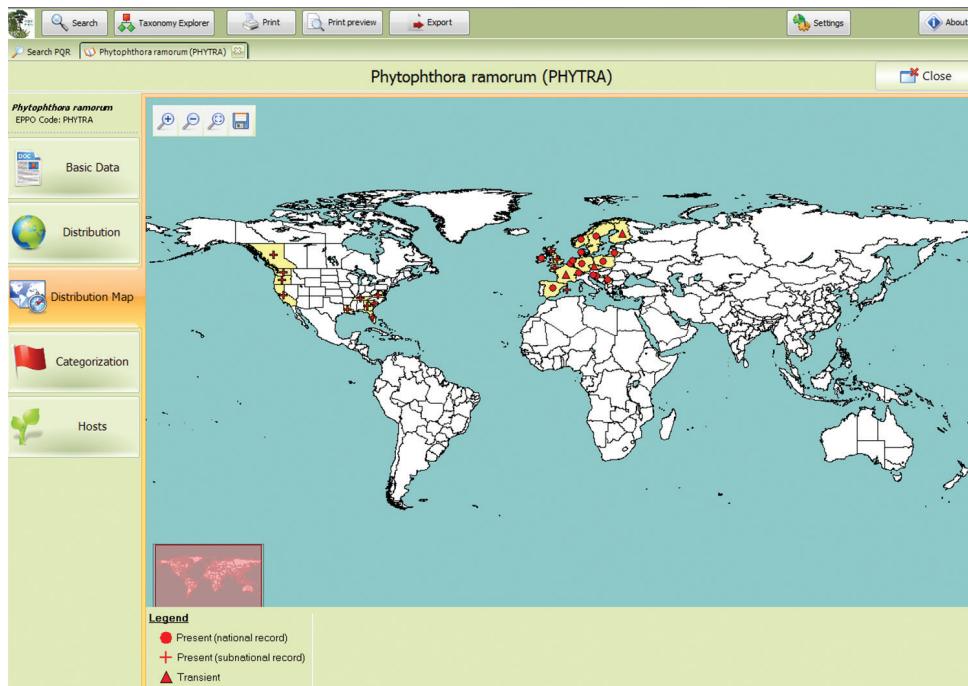


Figure 1. Global distribution of *Phytophthora ramorum* as shown by the EPPO Plant Quarantine Data Retrieval System.

alert list). Representing such information at such a large scale is not a trivial task as national records, sub-national records and the fact that a species is transient need to be shown on the map. The distribution records are represented as in the map displayed in Figure 1 for *Phytophthora ramorum*. Countries where the species is recorded are represented in yellow, to which is added a red circle when the record is provided at the national scale, a red cross when the record is provided at the sub-national level, and a red triangle when the species is transient. Maps are dynamic and updated when new data are available. References are provided to support distribution records.

In addition to mapping the global distribution of pests, EPPO models the potential distribution of pests when performing pest risk analyses.

EPPO modelling: performing pest risk analyses

EPPO Expert Working Groups on PRA

One of EPPO's main priorities is to prevent the introduction of dangerous pests (bacteria, fungi, insects, plants, viruses, etc.) from other parts of the world, and to limit their spread within the region should they be introduced. In recent years, trade networks have expanded and diversified, increasing the risks of introducing pests to new

geographical areas. Measures adopted by countries to protect their territories from these introductions should be technically justified and an International Standard for Phytosanitary Measures (ISPM) on Pest Risk Analysis (PRA) (ISPM 11) has been developed by the IPPC. Since the 1990s, developments have taken place within EPPO. A Panel on PRA development has been created. EPPO has developed a decision-support scheme for Pest Risk Analysis (EPPO 2011) and a computer program (CAPRA) to assist pest risk analysts in running the decision-support scheme. Expert Working Groups (EWGs) are now being convened to conduct PRAs on specific pests.

In order to share costs and workload and to provide technical justification for the regulation of certain pests, EPPO conducts PRAs for the region. Since September 2005, the EPPO PRAs have been produced by dedicated Expert Working Groups for PRA. Approximately five pests (including one invasive alien plant) are evaluated by expert working groups every year. The composition of the Expert Working Groups includes experts on the pest, on the crop/habitat of concern, in socio-economics, on running the EPPO PRA scheme and on tools to help assess the potential distribution of the pest (e.g. geographical information systems (GIS) and CLIMEX (Sutherst et al. 2007)) and perform risk mapping. Experts are invited by EPPO to the EPPO Headquarters in Paris for four days to conduct the Pest Risk Analysis. The PRA is based on the relevant bibliography and a draft PRA which is prepared and circulated to the experts beforehand by the EPPO Secretariat.

EPPO as an interface between pest risk science and policy

EPPO stands at the interface between pest risk science and policy. EPPO's procedures for the development and approval of standards and recommendations involve both risk assessors and risk managers at various steps of the process. This process facilitates communication between the two groups. This is illustrated in the way EPPO PRAs are performed and approved. After the scientists in the Expert Working Group have drafted the PRA, the document is reviewed by core members (experts nominated by EPPO countries' plant protection organizations to review the PRA produced) to ensure the consistency in the use of the EPPO decision-support scheme for PRA. Once this review is done, the PRA is presented to the EPPO Panel on Phytosanitary Measures (composed of experts with a management background). This Panel reviews the PRA focusing on risk management options. During both reviews, the Expert Working Group is consulted to answer questions arising from the PRA. A report of the PRA is then produced and presented to the Working Party on Phytosanitary Regulation (composed of representatives of NPPOs, but not heads, see below) which makes proposals to the EPPO Council (composed of heads of NPPOs) that the pest should be recommended for regulation (or not) and subsequently added to the lists of species recommended for regulation as quarantine pests.

EPPO also collects information from experts during its workshops and conferences. Such data are then used within EPPO Panels to develop standards (e.g. national

regulatory control systems), which are then reviewed and validated by risk managers and decision makers with the same groups as already mentioned above, i.e. the Panel on Phytosanitary Measures, Working Party and Council. EPPO's role as an interface between science and policy was particularly clear when taking part in the PRATIQUE EU Research project to improve the EPPO Decision-Support Scheme. EPPO also ensures that the exchange of information is bidirectional. Thus, in the framework of PRATIQUE, a survey was conducted to seek the feedback of decision makers on Pest Risk Analysis in the EU Plant Health Standing Committee (e.g. on the usefulness of ratings, the decision makers' perceptions of impacts, how to take time into account, how they would like climate change to be integrated in PRA, etc.). The outcomes of this survey were communicated to researchers so these could be taken into account when proposing new pest risk analysis methods.

The Decision-Support Scheme for climatic suitability risk mapping

Since 2011, the EPPO PRA scheme has been improved by integrating the outcomes of the European Research Project PRATIQUE (Enhancements of Pest Risk Analysis Techniques) which ran from 2008 to 2011 (Baker 2012). The improved methods included the assessment of economic, environmental and social impacts; summarizing risk using effective, harmonized and consistent techniques that take account of uncertainty; mapping endangered areas, pathway risk analysis and systems approaches; and guiding actions during emergencies caused by outbreaks of harmful pests.

The new version of the EPPO Decision-Support Scheme (DSS) is freely available, including its computerized version named CAPRA (see Griessinger et al. 2012 for a full description) that can be downloaded from the EPPO website (<http://capra.eppo.org/>). Questions and guidance related to mapping the area at highest risk and the endangered area have been included in the EPPO DSS as outlined by Eyre et al. (2012) and Baker et al. (2012a).

When assessing the probability of establishment of a pest, the assessor is requested to consider whether factors such as (i) host plants and suitable habitats, (ii) alternate hosts and suitable species, (iii) climatic suitability, (iv) competition and natural enemies, (v) the managed environment and (vi) protected cultivation are likely to have an influence on the limits of the area of potential establishment. Only the relevant factors are then considered to assess the limits and suitability of the endangered area.

For all these factors, guidance has been developed, and the relevant databases are listed in the CAPRA Datasets.

Emphasis has been given to assessing the climatic suitability of the environment in the PRA area. Rating guidance for climatic suitability is provided and links to maps useful in identifying the climates where the pest is present for comparison with the area under assessment are given. These include the CABI Crop Protection Compendium Pest Distribution and Climate Maps (<http://www.cabi.org/cpc/>), the Köppen-Geiger climate classification (Kottek et al. 2006) updated by Kriticos et al. (2012), the World

Hardiness Zones updated by Magarey et al. (2008) and the Global Maps of Temperature Accumulation (Degree Days) based on 10°C (Baker 2002).

In addition, a Climatic Suitability Risk Mapping Decision-Support Scheme (Eyre et al. 2012) has also been developed. It is intended for use by risk assessors who have already undertaken a qualitative assessment of the suitability of the climate for pest establishment. This DSS consists of a series of questions in five stages for which guidance and examples are provided.

Stage 1: ‘Is it appropriate to map climatic suitability?’

Stage 1 is designed to ensure that risk assessors carefully consider whether it is appropriate to devote time and resources to mapping climatic suitability when the assessment is already clear-cut or the information available is likely to produce results that are difficult to interpret and are therefore unhelpful to the assessment of pest risk.

Stage 2: ‘What type of organism is being assessed and what are the key climatic factors affecting distribution?’

Stage 3: ‘How much reliable information is available on the key climatic factors affecting distribution?’

Stage 4: ‘What category of location data is available?’

Stages 2–4 are used to review the information available on a pest’s climatic responses and its distribution.

Stage 5: ‘Based on the type of organism, the information available on its climatic responses and the category of location data, how well is each climatic mapping method likely to perform?’

Stage 5 outlines the implications of using each method based on the information assembled in stages 2–4.

Examples of how potential climatic suitability is modelled in the framework of EPPO PRAs

The new developments described above concerning the guidance to map the potential endangered area of a species were integrated into the EPPO DSS in 2011. The way the potential climatic suitability range has been assessed since these new developments is illustrated through two examples: *Thaumatomibia leucotreta* (Lepidoptera) and *Apriona germari* (Coleoptera).

Study of the area endangered in the EPPO region by *Thaumatomibia leucotreta* (Lepidoptera)

Basic elements on *Thaumatomibia leucotreta*

Thaumatomibia leucotreta is a polyphagous pest and has been recorded on many hosts present in the EPPO region. Significant hosts include citrus species, cotton and maize.

Damage is caused by larvae feeding in fruits, maize ears or cotton bolls. On citrus, the degree of damage is highly variable, but can reach up to 90%. The species is native and widespread in sub-Saharan Africa and also occurs on islands in the Atlantic and Indian Oceans (Madagascar, St. Helena, Cape Verde, Mauritius and Reunion). In the EPPO region, the species is only recorded in Israel.

Thaumatomibia leucotreta has 2–10 generations annually (Daiber 1980, Couilloud 1994, Begemann and Schoeman 1999). The number of generations is determined by several factors including temperature, food availability/quality, photoperiod, humidity, latitude and the effect of predators and diseases. In South Africa, during the summer, it can complete a generation in 45 days, while during the winter, development slows, although there is no actual diapause, and a generation takes about 100 days. In areas with a prolonged dry season, irrigation allows populations to build up to levels which can cause damage. For example, *Thaumatomibia leucotreta* was uncommon in Nigeria but became a major pest within 10 years of cotton irrigation being introduced into Nigeria in the 1960s (Glas 1991).

All hosts are widely grown over the EPPO region, and hosts are therefore not a limiting factor to the establishment of the species. Mapping hosts is therefore insufficient. Except for climate, no other abiotic factors are likely to have an influence on the limits of the endangered area and were not considered further (see EPPO Unpublished a).

Assessment of the climatic suitability of the EPPO region for *T. leucotreta*

For this assessment, it was decided to undertake a more detailed investigation than a visual comparison of global climate zones (i.e. the Köppen-Geiger climate classification, the World Hardiness Zones) to attempt to map the area of climatic suitability. The climatic suitability DSS (Eyre et al. 2012) was implemented.

It showed that, although *T. leucotreta* is present in the coastal plain of Israel, further investigation is needed to identify other areas that are climatically suitable in the EPPO region. *T. leucotreta*'s presence in the coastal plain of Israel indicates that some parts of the EPPO region are highly suitable climatically. The larval stage is protected within the fruit and the pupal stage may be in the soil but climate will still play a role in influencing survival. The species distribution is well known in sub-Saharan Africa. However, in the south-west of South Africa (Western Cape) the species is not considered to be native, there are only a few location records, and the southernmost limits to its distribution are set by the Indian and Atlantic Oceans. In addition, for year-round survival, the species needs fruits to be continuously available (although the species is polyphagous and can be found on alternate hosts such as nuts in the Cape).

Although the climatic suitability DSS indicated that the CLIMEX 'Compare locations' model (that predicts a species' potential distribution based on known climatic responses and its current known distribution) would have been an appropriate task to undertake, this model was not run due to lack of time and because too little is known about the factors influencing winter survival. In addition, the distribution in South

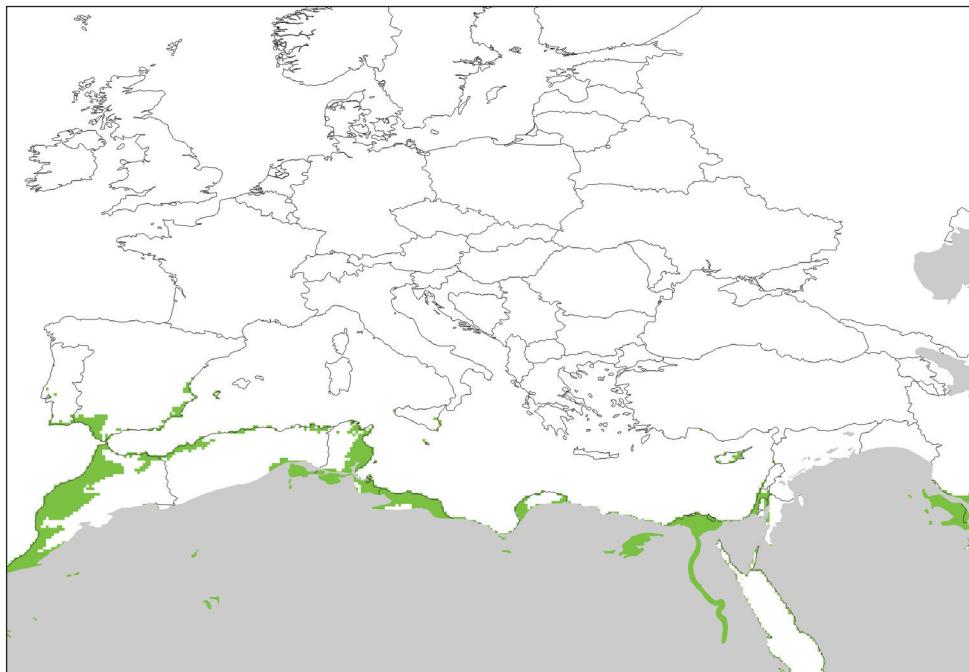


Figure 2. Non-desert areas of the EPPO region that are climatically suitable for *T. leucotreta*. This map is based on the relationship between maximum and minimum temperatures in the coldest month (July for the southern hemisphere and January for the northern hemisphere) based on: $T_{\min} \geq 1^{\circ}\text{C}$ and $T_{\max} \geq 18^{\circ}\text{C}$, or $T_{\min} \geq 3^{\circ}\text{C}$ and $T_{\max} \geq 15^{\circ}\text{C}$.

Africa is too strongly influenced by the presence of the sea and the requirement for a continuous food (fruit) supply to make it easy to infer the areas that are at the climatic limits of its distribution.

As a consequence, a simple rule based on diurnal temperatures (based on the difference between weekly maxima and minima) was adopted although it is recognised that this is based on very few locations (though these are considered to include the extremes in South Africa). Moreover, since there is uncertainty about the characteristics of the coldest winter that *T. leucotreta* can survive, this rule may identify only a minimum area of potential establishment when extrapolated to the EPPO region.

The maximum and minimum temperatures in South Africa and Israel (range limit of the species) were compared using the 1961–90 mean monthly minimum and maximum temperature interpolated to 10 minutes of latitude and longitude (New et al. 2002) and the similar Climond database (which contains global high resolution historical and future scenario climate surfaces for bioclimatic modelling, see www.climond.org) loaded into CLIMEX (Kriticos et al. 2012). It was assumed that the capacity to survive cold stresses during the winter is the key climatic factor influencing establishment of the species. The following rule fitted the different locations in South Africa: $T_{\min} \geq 1^{\circ}\text{C}$ and $T_{\max} \geq 18^{\circ}\text{C}$, or $T_{\min} \geq 3^{\circ}\text{C}$

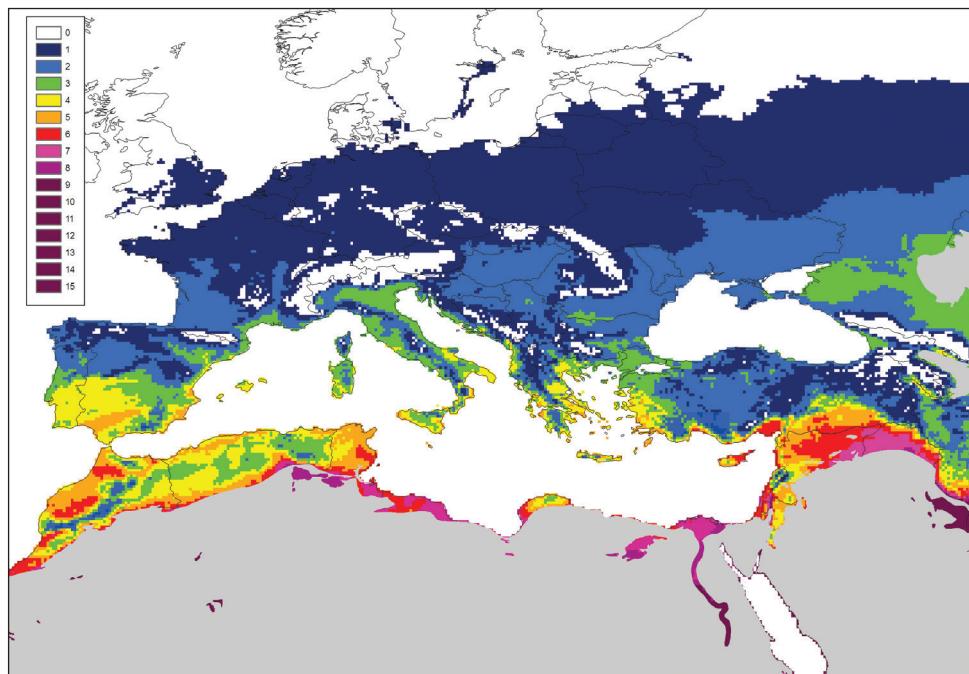


Figure 3. The number of generations for *T. leucotreta* possible in the EPPO region. This map is based on a minimum development threshold of 12°C and the number of degree days required for each generation of 433.

and $T_{max} \geq 15^\circ\text{C}$. This rule was therefore extrapolated to the EPPO region, and the desert regions which are not suitable for the species to survive were removed. As represented in Figure 2, the following countries were considered suitable for *T. leucotreta* to establish: Algeria, Cyprus, Israel, Italy, Jordan, Malta, Morocco, Portugal, Spain and Tunisia. An analysis of more recent meteorological data from southern Greece, e.g. Crete, showed that conditions are also suitable for establishment in this country.

The potential for transient populations to develop during summer was explored. As shown in Figure 3, this analysis found that one generation (assuming eggs are laid early in the summer) is possible as far north as the Baltic coast of Sweden, Latvia and central England. In southern coastal Mediterranean climates, up to seven generations may be possible. In key citrus growing areas such as Valencia (Spain), five generations may be possible. In the Canary Islands and the Azores (not pictured in Figure 3), three to six generations are possible.

The tools provided by the EPPO DSS for assessing and mapping climatic suitability, simplified appropriately for the analysis (Baker et al. 2012b, 2013), allowed a complex and thorough analysis for the area where the species could establish as well as where transient populations could be present. All details of this analysis are presented in the Pest Risk Analysis for *Thaumatomibia leucotreta* (EPPO 2012a).

Study of the endangered area in the EPPO region of *Apriona germari* (Coleoptera)

Basic elements on *Apriona germari*

Apriona germari is an important pest of broadleaved trees. Seventy plant species of hosts are reported (from Betulaceae, Cornaceae, Ericaceae, Euphorbiaceae, Fabaceae, Fagaceae, Moraceae, Rosaceae, Salicaceae, Ulmaceae and other families). In its native area, this species causes significant economic damage (Huang et al. 1996). Many of its hosts are important commercial, ornamental or forest trees in the EPPO region. The life cycle of the species generally lasts one year in warm climates (tropical parts of China) and two to three years in cooler areas. The main damage associated with *A. germari* is caused by the larvae, which bore into the wood soon after hatching, creating long tunnels. This affects the growth of the trees and decreases the quantity and quality of the timber and the longevity of the trees (Shui et al. 2009; Li 1996).

A. germari is distributed in a large number of Asian countries (including Cambodia, China, India, Korea, Laos and Thailand). Although the species is believed to have originated in Asia, its exact native range is unknown. *A. germari* has been intercepted by countries in the EPPO region and in the USA on a number of occasions, and in particular in the Netherlands in 2008 and 2009, which triggered the production of a Dutch PRA (Ibáñez Justicia et al. 2010). The species is still absent from the EPPO region.

The presence of hosts, the climate and the managed environment are factors which affect the extent of the area endangered by *A. germari* in the EPPO region. As large numbers of host species are of interest, global distribution maps of the main hosts, *Ficus carica*, *Malus domestica* and *Pyrus* spp., have been consulted and included in the PRA adapted from Monfreda et al. (2008). Maps of *Populus nigra*, *Populus tremula* and *Pyrus pyraster* have been consulted and included in the PRA from the EUFORGEN programme (http://www.euforgen.org/distribution_maps.html). It was concluded that hosts are not a limiting factor for establishment, but that the Mediterranean area may be most suitable as host plants are more widespread.

Assessment of the climatic suitability of the EPPO region for *A. germari*

To evaluate the climatic suitability of the EPPO region, the assessment was strongly based on the existing Dutch CLIMEX 'Compare Locations' model (Ibáñez Justicia et al. 2010). Some data on development times were available in Yoon and Mah (1999). As there is a lack of data on the biological characteristics of the species, developmental temperature thresholds were extrapolated from available data for *Apriona japonica* (Kitajima et al. 1997). The Dutch PRA modelled the potential distribution of *A. germari* based on its distribution in China and two scenarios for the biology of the species relevant to the climates of the EPPO region: a 3 year life-cycle and a 2 year life-cycle. As shown in Figure 4 which shows the results for a 3 year life-cycle (which represents the scenario that will lead to the largest area of potential establishment), this analysis found that the following countries of the EPPO Mediterranean area are at risk: Albania, Algeria, Bulgaria, Croatia, Cyprus, France, Greece, Israel, Italy, Jordan, Malta, Morocco, Portugal, Spain, Tunisia and Turkey.

In addition, maps of temperature accumulation in degree days have been compared for Asia and Europe and are shown in Figure 5.

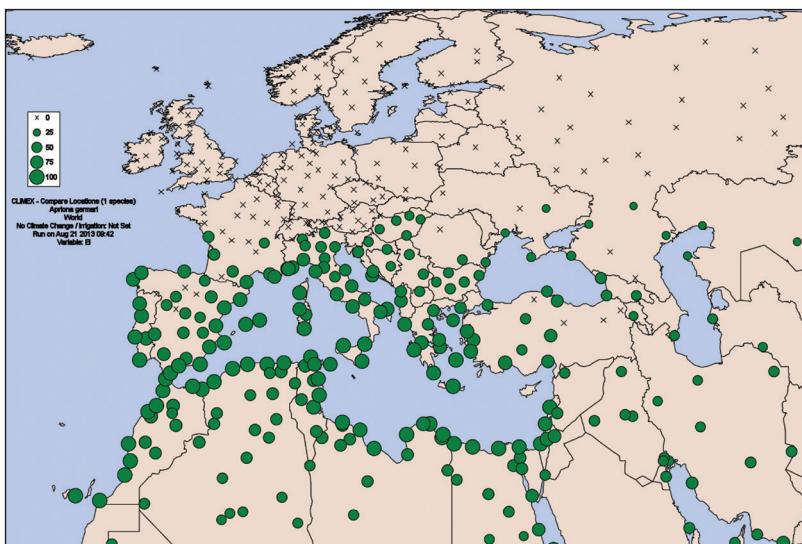


Figure 4. Potential distribution of *Apriona germari* in Europe based on a CLIMEX model with the hypothesis of a 3 year life cycle (1295 DD/year). The Ecoclimatic index (EI) indicates the climatic suitability for establishment. Crosses indicate unsuitable locations (EI=0). Green dots indicate the degree of climate suitability. The minimum threshold temperature for development in all models was 12 °C, based on Ibáñez et al. (2010).

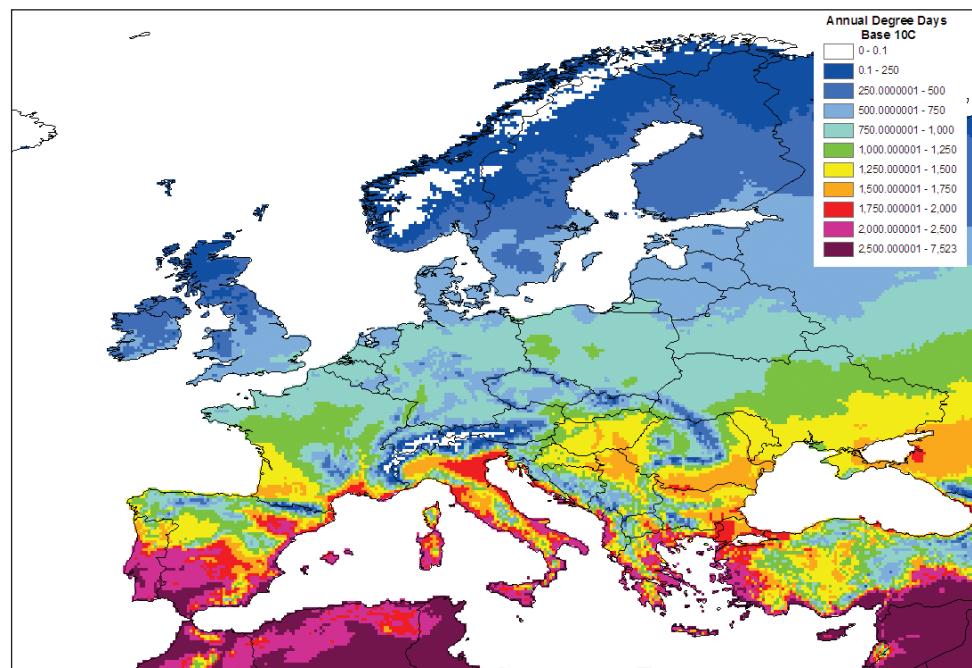


Figure 5. European Map of Temperature Accumulation (Degree Days). This map is based on a minimum threshold temperature for development of 10 °C, using 1961–90 monthly average maximum and minimum temperatures taken from the 10 minute latitude and longitude Climatic Research Unit database (New et al. 2002).

As for *T. leucotreta*, careful attention had been given to the assessment of the area of potential establishment by *Apriona germari*. Although hosts and climatic maps were not superimposed, the available maps have been gathered. All details of this analysis are presented in the Pest Risk Analysis for *Apriona germari* (EPPO Unpublished b).

Conclusions and further directions

EPPO, as a regional plant protection organization, plays a major role in PRA and stands at the forefront of practical application in this field by integrating a detailed climatic mapping DSS in its PRA processes. The maps of pest risk analyses are used to support recommendations to member countries concerning the pests and phytosanitary measures that can be added to their regulations.

Mapping and modelling nevertheless remain very difficult exercises, limited by available expertise, time and data related to the species being assessed. It is thus essential for an assessor to be trained and to regularly perform climate studies. EPPO organizes training courses to risk assessors to increase their modelling expertise in the EPPO region. Training courses have therefore been organized on CLIMEX in Spain and in France in 2008 and 2010 respectively. As CLIMEX demands a relatively high level of expertise, 'Instructions for the Use and Interpretation of CLIMEX' were developed by PRATIQUE (Baker et al. 2011). It is also to be noted that although the two examples presented here used the software CLIMEX, it is also possible to use other models such as MAXENT or OPENMODELLER in the EPPO DSS.

EPPO Expert Working Groups for PRA take advantage of models that have already been performed on the pest being assessed. In the case of *Apriona germani*, the EPPO PRA was built on the Dutch PRA CLIMEX model. This highlights the need for existing models on pests to be shared and circulated so as to combine and not duplicate efforts. The development of a database centralizing existing publications and PRAs on pest climatic models would be of great relevance and use.

Furthermore, modelling is a highly technical task. While modellers may understand the limits of models and of the maps they produce, risk managers may interpret the maps differently and may get a false sense of certainty. Uncertainty is assessed for each question in the EPPO PRA scheme, including climatic suitability, and given a low, medium or high score, but no straightforward method for representing uncertainty in maps has been identified. Climatic requirements are very often mentioned as a key component of uncertainty in PRAs. This emphasizes the importance of considering the level of understanding of maps by readers and the need for further enhancements of risk communication.

In addition to the modelling of pest distributions in PRA, other sectors may lead to future developments in the field of mapping. Citizen science for the surveillance and reporting of pests and invasive alien species is gaining increased attention. At the European scale, the European Environment Agency intends to adapt the 'Eye on Earth' initiative to invasive alien species (<http://www.eyeonearth.org/en-us/Pages/Home>).

aspx). Citizens would then be invited to provide data on the presence of particular invasive alien species which are already present in Europe and are sufficiently conspicuous and easy to identify. National projects have also been implemented with success. In Belgium, the Walloon region launched a citizen survey of the invasive alien plant *Heracleum mantegazzianum*. *H. mantegazzianum* is the tallest Apiaceae in the world as it grows up to 3 m high. Data provided by citizens are then displayed on a Google map which can be zoomed (<http://environnement.wallonie.be/berce/>). Norway is also developing such a citizen project (Rafoss et al. 2013). In the United Kingdom, 'Plant Tracker', a project launched by the Environment Agency, the University of Bristol and the Centre for Ecology and Hydrology developed an iPhone application to track the locations of three invasive alien plants in the country: *Fallopia japonica*, *Impatiens glandulifera* and *Hydrocotyle ranunculoides* (<http://planttracker.naturelocator.org/>). All aggregated data are then displayed on a map at the scale of the United Kingdom. Such innovative initiatives and the mapping skills and software required need further development by the International Pest Risk Mapping Workgroup as part of its roadmap for improving the pest risk mapping process (Venette et al. 2010).

Acknowledgments

We wish to acknowledge the chairs and organizers of the International Pest Risk Mapping Workgroup, namely Rob Venette, Darren Kriticos, Frank Koch, Trond Rafoss, Wopke van der Werf, and Richard Baker. The work of the participants of the EPPO Expert Working Groups on *Thaumatomibia leucotreta* and *Apriona germari* was indispensable material for this article, and we thank them all. We would also like to thank the OECD Co-operative Research Programme for sponsoring the meeting.

References

- Baker RHA (2002) Predicting the limits to the potential distribution of alien crop pests. In: Hallman GJ, Schwalbe CP (Eds) *Invasive Arthropods in Agriculture. Problems and Solutions*. Science Publishers Inc. Enfield USA: 207–241.
- Baker RHA, Brunel S, MacLeod A, Kriticos D (2011) Instructions for the Use and Interpretation of CLIMEX. Annex 2G, Deliverable 3.3 Protocol for mapping endangered areas: 1–10. www.pratiqueproject.eu
- Baker RHA (2012) An introduction to the PRATIQUE Research Project. Bulletin OEPP/EPPO Bulletin 42: 1–3.
- Baker RHA, Benninga J, Bremmer J, Brunel S, Dupin M, Eyre D, Ilieva Z, Jarosik V, Kehlenbeck H, Kriticos DJ, Makowski D, Pergl J, Reynaud P, Robinet C, Soliman T, Van der Werf W, Worner S (2012a) A decision-support scheme for mapping endangered areas in pest risk analysis. Bulletin OEPP/EPPO Bulletin 42: 65–73.

- Baker RHA, Eyre D, Brunel S (2013) Matching methods to produce maps for pest risk analysis to resources. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. *NeoBiota* 18: 25–40. doi: 10.3897/neobiota.18.4056
- Eyre DR, Baker RHA, Brunel S, Dupin M, Jarošík V, Kriticos DJ, Makowski D, Pergl J, Reynaud P, Robinet C, Worner S (2012) Rating and mapping the suitability of the climate for pest risk analysis. *Bulletin OEPP/EPPO Bulletin* 42(1): 48–55.
- EPPO (2011) PM 5/3 (5) Guidelines on Pest Risk Analysis. Decision-support scheme for quarantine pests, 1–44. <http://archives.eppo.int/EPPOStandards/pras.htm>
- EPPO (Unpublished a) Pest Risk Analysis for *Thaumatomibia leucotreta*. To be approved and published in 2013.
- EPPO (Unpublished b) Pest Risk Analysis for *Apriona germari*, *A. japonica*, *A. cinerea*. To be approved and published in 2013.
- Glas M (1991) Tortricids in miscellaneous crops. In: van der Geest, van Luis (Eds) Tortricoid Pests, Their Biology, Natural Enemies and Control. World Crop Pests: 5. UK: Elsevier.
- Griessinger D, Suffert M, Brunel S, Petter F (2012) CAPRA: the EPPO Computer Assisted PRA scheme. *Bulletin OEPP/EPPO Bulletin* 42: 42–47.
- Huang D, Yan J, Hu Y (1996) Geographical Distribution of *Apriona germari* in China. *Hebei Journal of Forestry and Orchard Research* 1996-z1. [Abstract]
- Ibáñez Justicia A, Potting R, van der Gaag DJ (2010) Pest risk assessment *Apriona* spp. Plant Protection Service, Ministry of Agriculture, Nature and Food Quality, the Netherlands, 1–27.
- Kitajima H, Hashimoto M, Makihara H (1997) Number of eggs oviposited by adults and relation between temperature and development of eggs and larvae of the mulberry borer, *Apriona japonica* Thomson. Proceedings of the 108th Annual Meeting of the Japanese Forestry Society, 379–380. [in Japanese]
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of Köppen- Geiger climate classification updated. *Meteorologische Zeitschrift* 15: 259–263. doi: 10.1127/0941-2948/2006/0130
- Kriticos DJ, Webber BL, Leriche A, Ota N, Macadam I, Bathols J, Scott JK (2012) CliMond: global high resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution* 3: 53–64. doi: 10.1111/j.2041-210X.2011.00134.x
- Li K (1996) Poplar stem-boring pests and their control. *J. Northeast For. Univ.* 7(1): 51.
- Magarey RD, Borchert DM, Schlegel JW (2008) Global plant hardiness zones for phytosanitary risk analysis. *Scientia Agricola* 65: 54–59. doi: 10.1590/S0103-90162008000700009
- Monfreda C, Ramankutty N, Foley JA (2008) Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. *Global Biogeochemical Cycles* 22: 1–19. doi: 10.1029/2007GB002947
- New M, Lister D, Hulme M, Makin I (2002) A high-resolution data set of surface climate over global land areas. *Climate Research* 21: 1–25. doi: 10.3354/cr021001
- Rafoss T, Skahjem J, Johansen JA, Johannessen S, Nagothu US, Fløistad IS, Sletten A (2013) Improving pest risk assessment and management through the aid of geospatial information technology standards. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models

- to address climate change, economics and uncertainty. *NeoBiota* 18: 119–130. doi: 10.3897/neobiota.18.4017
- Shui SY, Wen JB, Chen M, Hu XL, Liu F, Li J (2009) Chemical control of *Apriona germari* (Hope) larvae with zinc phosphide sticks. *Forestry Studies in China* 11(1): 9–13.
- Sutherst RW, Maywald GF, Kriticos D (2007) CLIMEX Version 3: Users Guide. Hearne Scientific Software Pty Ltd, Melbourne. <http://www.hearne.com.au/attachments/Climex-UserGuide3.pdf>
- Venette RC, Kriticos DJ, Magarey RD, Koch FH, Baker RHA, Worner SP, Gomez R, Nadilia N, McKenney DW, Dobesberger EJ, Yemshanov D, De Barro PJ, Hutchison WD, Fowler G, Kalaris TM, Pedlar J (2010) Pest risk maps for invasive alien species: a roadmap for improvement. *Bioscience* 60: 349–362. doi: 10.1525/bio.2010.60.5.5
- Yoon HJ, Mah YI (1999) Life cycle of the mulberry longicorn beetle, *Apriona germari* Hope on an artificial diet. *Journal of Asia-Pacific Entomology* 2(2): 169–173. doi: 10.1016/S1226-8615(08)60046-1

Matching methods to produce maps for pest risk analysis to resources

Richard H.A. Baker¹, Dominic Eyre¹, Sarah Brunel²

1 Food and Environment Research Agency, Sand Hutton, York YO41 1LZ, United Kingdom **2** European and Mediterranean Plant Protection Organization (EPPO/OEPP) - 21 boulevard Richard Lenoir 75011 PARIS- France

Corresponding author: Richard H.A. Baker (richard.baker@fera.gsi.gov.uk)

Academic editor: Rob Venette | Received 27 September 2012 | Accepted 3 June 2013 | Published 13 September 2013

Citation: Baker RHA, Eyre D, Brunel S (2013) Matching methods to produce maps for pest risk analysis to resources. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 25–40. doi: [10.3897/neobiota.18.4056](https://doi.org/10.3897/neobiota.18.4056)

Abstract

Decision support systems (DSSs) for pest risk mapping are invaluable for guiding pest risk analysts seeking to add maps to pest risk analyses (PRAs). Maps can help identify the area of potential establishment, the area at highest risk and the endangered area for alien plant pests. However, the production of detailed pest risk maps may require considerable time and resources and it is important to match the methods employed to the priority, time and detail required. In this paper, we apply PRATIQUE DSSs to *Phytophthora austrocedrae*, a pathogen of the Cupressaceae, *Thaumetopoea pityocampa*, the pine processionary moth, *Drosophila suzukii*, spotted wing Drosophila, and *Thaumatotibia leucotreta*, the false codling moth. We demonstrate that complex pest risk maps are not always a high priority and suggest that simple methods may be used to determine the geographic variation in relative risks posed by invasive alien species within an area of concern.

Keywords

Pest risk mapping, area of potential establishment, area at highest risk, endangered area, *Phytophthora austrocedrae*, *Drosophila suzukii*, *Thaumatotibia leucotreta*, *Thaumetopoea pityocampa*

Introduction

Pest risk analysis (PRA) provides the context for this paper. PRA is fundamental to plant biosecurity because it is primarily undertaken to assess the risks posed by plant pests that are not officially established in an area and to identify appropriate phytosanitary measures to prevent entry and establishment if the risk is unacceptable. Pest risk analyses that may affect international trade should follow international standards for phytosanitary measures (especially ISPM 11; FAO 2004) because they have been formulated by the International Plant Protection Convention and are recognised by the World Trade Organization. Although the international standards set out clearly what elements need to be assessed in order to evaluate the likelihood of entry and establishment together with the magnitude of spread and impacts, they do not provide clear guidance on the methods to be used in completing the PRA. As a result, a number of schemes have been created to assist pest risk analysts with the production of PRAs based on expert judgement and documented evidence. For example, the European and Mediterranean Plant Protection Organization (EPPO) provides a well known scheme to guide the production of PRAs through a series of questions that require answers in the form of a risk rating, an uncertainty score, and a written justification (EPPO 2011).

The EPPO PRA scheme has recently been enhanced by PRATIQUE, an EU funded research project (Baker et al. 2009), by providing several guidance documents and tools, for example, guidance for rating the level of risk (Schrader et al. 2012) and a computerised procedure for completing the PRA (Griessinger et al. 2012). Additional modules are available to help when it is important for pest risk analysts to quantify risk spatially or at least provide greater detail for particular components of the PRA. These include a decision support system (DSS) for mapping climatic suitability, summarised in Table 1 (Eyre et al. 2012) and a DSS for mapping endangered areas (Baker et al. 2012), the topic of this paper.

Maps provide an important method for visualising, summarising and communicating the risk posed by a pest in the PRA area that can be an officially defined country, part of a country or all or parts of several countries (FAO 2012). Within the PRA area, three different risk areas can be identified by pest risk analysts. These are: (i) the area of potential establishment, where it is likely that there is “perpetuation, for the foreseeable future, of a pest within an area after entry” (FAO 2012); (ii) the endangered area, where “ecological factors favour the establishment of a pest whose presence in the area will result in economically important loss” (FAO 2012) and (iii) the area at highest risk, where impacts are assessed as likely to be greatest, e.g. because particularly valuable or vulnerable hosts are growing in areas where abiotic and biotic factors are most suitable for the pest. Economic loss in the endangered area definition is considered to include environmental damage (FAO 2012). Although areas at risk can be described just by listing the geographical regions that are included, maps can convey a clearer message. Maps can also be deployed to help target eradication and containment actions in the event of an outbreak and set up an effective surveillance programme.

Table 1. Summary of the PRATIQUE climatic mapping decision support scheme.

Stage	Tasks	Detail
1	Decide whether mapping climatic suitability is appropriate	Based on available data for mapping and importance of the pest
2	Gather and interpret key climatic factors affecting distribution	Determine which data sets are important for the pest
3	Determine the quality and quantity of information that is available on the key climatic factors	Provide a rating based on availability and reliability
4	Categorise location data	Diagrams are provided to help the assessor to choose from 13 categories of location data
5	Evaluate pros and cons of different climatic mapping methods	Use tables to show possible drawbacks of the different methods available based on the ecology of the pest and the data available

Although many PRAs already contain maps depicting components of pest risk that have been created without formal models and geographical information systems (GIS), most profit from such tools. Frequently, the PRA just includes a map of climatic suitability. Climatic suitability needs to be combined with factors such as host or habitat distribution firstly to obtain the area of potential establishment and secondly with impact related components, such as host or habitat vulnerability and value, to map the areas at highest risk. NAPPFAST provides a suite of interconnected models that can be used individually or collectively with tailored climatic data to map pest risk for North America (Magarey et al. 2007, 2011). Outputs from the PRATIQUE DSS for mapping climatic suitability (Eyre et al. 2012) and the area of potential establishment and highest risk (Baker et al. 2012) can be linked to models of spread (Kehlenbeck et al. 2012) and economic impact (Soliman et al. 2012) to map the dynamics of invasion and impact scenarios that illustrate possible endangered areas. The DSSs are independent of the models used and the area of concern, although the examples are provided for all or parts of Europe.

The PRATIQUE DSS described by Baker et al. (2012) focuses on identifying the area of potential establishment and the area at highest risk rather than endangered areas. This is because a map of the endangered area should show only where economically important loss is predicted to occur and this is very difficult given the uncertainty surrounding all pest invasions together with the need to predict pest population densities and relate these to poorly defined economic injury levels (Pedigo et al. 1986) while taking into account the effectiveness of pest management practices. Since the areas at highest risk from economic, environmental or social impacts can be mapped without modelling population densities in relation to economic thresholds it is therefore more practical to follow this approach not only to provide evidence supporting the PRA but also to help target actions following outbreaks and to design effective surveillance programmes and contingency plans.

Methods for combining maps of climatic suitability, host distribution, and host value with a simple mapping program (ABARES 2012) are summarised by Baker et al. (2012). The DSS has an introduction and four further stages, see Table 2.

In stage 1, the key factors that influence the endangered area are identified by using the biological, ecological and agronomic information in the pest risk assessment, the geographic data sets are assembled and, where appropriate, maps of the key factors are produced listing any significant assumptions. In stage 2, methods for combining these maps to identify the area of potential establishment and the area at highest risk from pest impacts are described, documenting any assumptions and combination rules utilised. When possible and appropriate, stage 3 can then be followed to show whether economic loss will occur in the area at highest risk and to identify the endangered area. As required, stage 4, provides techniques for producing a dynamic picture of the invasion process using a suite of spread models. Baker et al. (2012) illustrate the functioning of the DSS with two pests: the maize insect pest, *Diabrotica virgifera virgifera*, and the aquatic invasive alien plant, *Eichhornia crassipes*. For both these species, extensive information and maps are available on, e.g. climatic responses and host/habitat distribution, and there was ample time and resources for the analyses. A comprehensive description of the DSS is available in the project report (Baker et al. 2011).

In this paper, we apply the area mapping DSS to four case studies to determine the need for pest risk maps. We propose simple, quick analyses (i.e., shortcuts) to answer questions posed by the DSS and suggest these shortcuts could be particularly useful when risk maps are needed urgently, when an incursion threat seems imminent, or an outbreak has been detected. In addition, many plant health services have limited staff with skills in pest risk mapping and modelling and are faced with budget reductions. If used appropriately, the DSS can guide the production of exploratory pest risk maps created with relatively little time and resources. These exploratory analyses can still be helpful and, at minimum, can justify the need for a more detailed analysis and additional funding.

Table 2. Summary of the PRATIQUE endangered areas decision support scheme.

Stage	Tasks	Detail
Introduction	Decide whether mapping the endangered areas is going to be possible and useful	Based on the value of additional information that this process is likely to lead to and the data available
1	Confirm the factors that influence the endangered area	Describe the area of potential establishment, gather all appropriate data including maps that can influence the endangered area. Put maps into the same resolution and enter into the mapping software MCAS
2	Combine maps to determine areas of potential establishment and areas of highest risk	Guidance is given on how to combine the different data sets to obtain the relevant maps
3	Combine maps to determine endangered areas	Guidance is provided on the application of spread models
4	Optional module to evaluate rate of spread	Guidance is provided on the application of spread models

The rationale for shortcuts

It is important to tailor efforts according to the priority for which pest risk mapping is needed to provide support for the PRA. Although strict rules cannot be set because maps provide other important functions, we have attempted to identify situations of high and low priority.

High priority situations

In the main, pest risk maps are more useful when the potential for invasive alien species to establish and thrive in the PRA area is highly uncertain. Thus, the highest priorities for pest risk mapping are generally for those species that also require the most attention to detail, e.g. because impacts could be high but the likelihood is uncertain. This could occur when the likelihood of establishment is considered to be uncertain but, if establishment were to occur, the magnitude of impact is expected to be high because the measures available for eradication and containment would be limited and expensive.

Low priority situations

Risk maps can be considered to be a low priority without detailed analysis when it is already clear that:

- widespread establishment is likely, e.g. because the pest is common in neighbouring areas with similar climates and hosts or because pest outbreaks have already occurred within the PRA area demonstrating the potential for establishment and indicating that harmful impacts are likely to be uniformly distributed.
- the area of potential establishment can be identified without risk mapping, e.g. because establishment is only possible on hosts with a well defined and mapped distribution in discrete habitats or crop production systems, such as protected cultivation, and harmful impacts are likely to be uniformly distributed.

In addition to taking these priorities into account when deciding whether or not to map risk, it is also important to identify and apply any shorter or simpler methods of mapping when there is little time (for example, because an outbreak has occurred and emergency action is required in an area where the pest is not established), resources are limited, (for example, because of budgetary cuts or a lack of staff experienced in risk mapping) or the priority for risk mapping is relatively low. We therefore indicate where short cuts may be possible and discuss the implications for the PRATIQUE area mapping DSS.

To show how these priorities and the amount of detailed analysis required can match up when undertaking PRAs, four examples based on recent work by EPPO and by the Food and Environment Research Agency (FERA) and Forest Research in the UK representing a range of risk and uncertainty are explored in this paper.

Case studies

Phytophthora austrocedrae (Oomycetes: Pythiaceae) in the United Kingdom

This pathogen of Cupressaceae originates from Argentina and Chile and has recently been found in the UK on juniper (*Juniper communis*), Lawson cypress (*Chamaecyparis lawsoniana*) and Nootka cypress (*Chamaecyparis nootkatensis*) (Forestry Commission 2013). It is established outdoors, particularly in north-west England and western Scotland. Forest Research (2012) undertook a rapid PRA on *P. austrocedrae* for consultation to assess its risk to the UK. It concluded that the climate is suitable for establishment throughout the UK and that environmental impacts are potentially significant because of the importance of juniper for biodiversity (JNCC 2007). For this species there was no need to produce climatic suitability maps and so the climatic mapping DSS could be ignored.

Since the climate is suitable for establishment throughout the UK, the area of potential establishment can be considered to be equivalent to the distribution of *J. communis* in uncultivated areas and the ornamental Cupressaceae hosts in parks and gardens. Maps of the distribution of *J. communis* and its subspecies are available from the National Biodiversity Network (see Figure 1) and the Botanic Society of the British Isles (Lockton 2012). The endangered area for environmental impacts can be represented by mapping the 1,100 ha of juniper in areas of Special Scientific Interest (JNCC 2007). This pest can therefore be considered a low priority for pest risk mapping because pest outbreaks have already occurred in the UK demonstrating the high potential for establishment and indicating that harmful impacts are likely to occur wherever juniper grows.

Drosophila suzukii (Diptera: Drosophilidae) in Europe

This small fly lays its eggs in a wide variety of ripe and unripe soft skinned fruit and can cause significant damage (Lee et al. 2011). It originates from Eastern Asia and in 2008 it was first found in several locations in Europe (Calabria et al. 2012) and North America (Hauser 2011). In 2010, EPPO conducted a PRA and concluded that this species can establish in a wide area of the EPPO region because its hosts are ubiquitous and only the coldest and most arid climatic zones are unsuitable for survival; economic impacts could occur wherever the pest can establish (EPPO 2011).

Although considerable efforts were made to find and map all the locations where *D. suzukii* had been recorded and to search the literature for any records of climatic responses, these conclusions were based on a relatively simple analysis. *D. suzukii* can survive the long cold winters at its northern limits to its distribution in northern China through its association with human habitation. Since such severe winters occur very rarely in Europe and hosts are very widespread, the principal factor determining its northerly limits in Europe was considered to be the amount of degree days available for development and reproduction. A simple phenology model with a base temperature of 10°C and 250

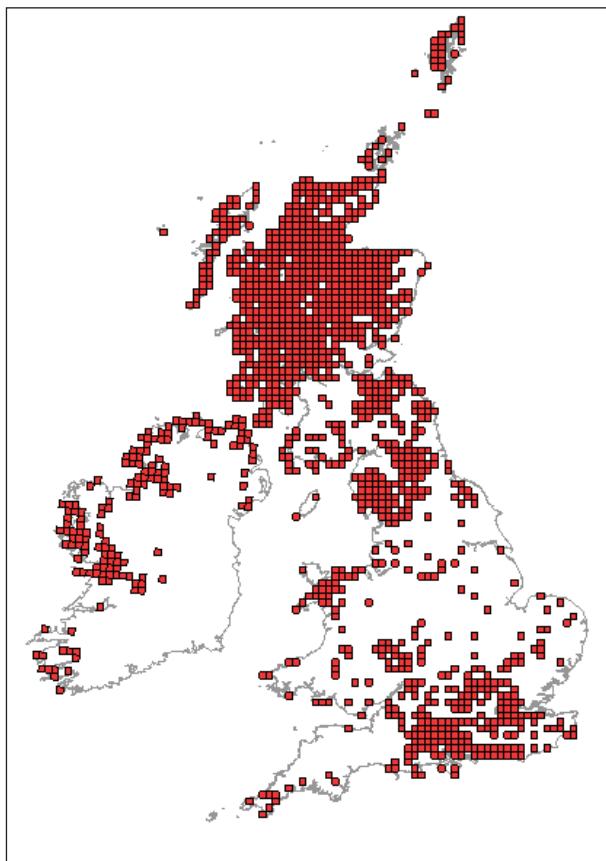


Figure 1. Distribution of *Juniperus communis* in Great Britain and Ireland from the National Biodiversity Network Gateway (NBN Gateway: data.nbn.org.uk) © Crown copyright and database rights 2011 Ordnance Survey [100017955]

degree days was therefore applied to the 1961-90 Climatic Research Unit monthly gridded climatology at 30 minute latitude and longitude resolution (New et al. 2002) and mapped (see Figure 2). Only extreme northern and mountainous areas were found to be unsuitable. Elsewhere there are sufficient accumulated degree days for numerous generations to be completed in the summer. Since oviposition in unripe fruit allows pathogens to enter and causes a serious loss of quality, the presence of *D. suzukii* populations is likely to cause economic loss and the endangered area can be considered to be equivalent to the area where host crops are grown in the area of potential establishment. This pest can therefore be considered a low priority for pest risk mapping in most of Europe because widespread establishment is very likely and pest outbreaks have already occurred demonstrating the high potential for establishment and indicating that harmful impacts are likely to be uniformly distributed. Therefore, on a European scale, the endangered area DSS is not relevant. However, more detailed mapping at the limits to its distribution in Scandinavia and at high altitude is of higher priority and would be justified.



Figure 2. The area (in green) where annual degree day accumulations above a base temperature of 10°C exceed 250 with the locations of *Drosophila suzukii* known in August 2010 (in red).

***Thaumatotibia leucotreta* (Lepidoptera: Tortricidae) in Europe**

This polyphagous fruit pest, the false codling moth, is native to sub-Saharan Africa and can be particularly damaging to a variety of fruits including oranges and peaches. As summarised by Brunel et al. (2013), EPPO undertook a limited climatic analysis on this species as part of a detailed PRA. As with *D. suzukii*, substantial efforts were taken to obtain as many distribution records as possible and collect information on its climatic responses from the literature but climate suitability models, such as CLIMEX, were not employed. This was partly due to lack of time and partly because its presence in the Israeli coastal plain had already demonstrated its ability to establish in the EPPO region. However it was also because the factors influencing winter survival are poorly known and the distribution in South Africa is strongly influenced by non-climatic factors.

A simple rule based on the difference between maximum and minimum winter temperatures above a minimum threshold fitted both the limits to the distribution in South Africa and the area in Israel where it is established. The maps generated by applying this rule to global climatologies could therefore be used to define the area of potential establishment, especially because the hosts, e.g. *Ricinus communis* (castor oil plant), are widespread in southern Mediterranean coastal areas. Areas of highest risk occur where the crops of major economic importance, such as oranges, are grown

in the area of potential establishment. This pest can therefore be considered a relatively high priority for pest risk mapping in the EPPO Region. Outbreaks have already occurred in one area (Israel) demonstrating that establishment is possible, but more detailed mapping is required to explore the limits to its distribution in southern Europe. The mapping needs to take into account the magnitude of the potential impact together with the feasibility and expense of eradication and containment.

***Thaumetopoea pityocampa* (Lepidoptera: Thaumetopoeidae) in the United Kingdom**

This pest, the pine processionary moth, defoliates *Pinus* species and the larval hairs can cause severe skin rashes and eye damage. Since it is widespread in the Mediterranean area and is spreading northwards in France assisted by climate change (Robinet et al. 2011), FERA undertook a rapid PRA for consultation (FERA 2012a) for the UK. This PRA showed that, although establishment is unlikely, there is a high uncertainty and a more detailed analysis is required because of the potential for severe impacts. This conclusion was justified by some exploratory analysis. Maps of the main *Pinus* hosts in the UK were obtained from the Botanic Society of the British Isles (BSBI 2012) and visually compared with maps of mean minimum and maximum winter temperatures and sunshine duration for 1971–2000 (UK Meteorological Office 2012a). Coastal central southern England was found to have the highest diversity of host *Pinus* species in the UK and the warmest, sunniest winters. Survival at the northern edge of its range in France is related to nest temperatures (maximum daily temperature and solar radiation) which is correlated with mean minimum winter temperatures (Robinet et al. 2007). FERA therefore (2012a) compared the mean minimum winter (October to March) temperatures over the last twenty years at one location in coastal central southern England (Hurn Airport, 50.7800°N, 1.8425°W) with those in Orleans and Paris where the pest has established damaging pest populations (see Figure 3). The similarity in the winter minimum temperatures at Hurn Airport and Orleans suggests that parts of southern coastal England have sufficient warmth to sustain populations of PPM. Thus for a rapid comparison of the climatic conditions in locations where the pest found and the most southerly locations in England was able to demonstrate some risk. The host distribution provided an indication of the areas at highest risk. These simple methods were sufficient to demonstrate the need for further analysis without the use of either of the DSSs. For this pest the area of potential establishment is still very uncertain and further work is required to try and resolve the uncertainties concerning, for example whether there is sufficient solar radiation for survival in southern England. This pest can therefore be considered a high priority for pest risk mapping because the likelihood of establishment in even a small area of the UK where host crops are grown is considered to be very uncertain but, if establishment was to occur, the magnitude of impact is expected to be high.

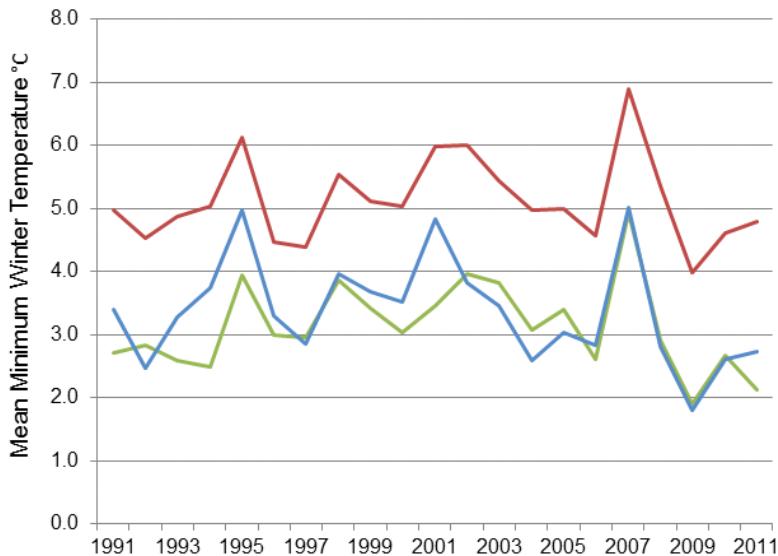


Figure 3. Mean minimum (October - March) temperatures from 1991–2011 for one location in southern UK (Hurn Airport) (coloured in green) with Orleans (blue) and Paris (red) in France. Data were obtained from the UK Meteorological Office (2012b) and from the Ensembles project (<http://eca.knmi.nl/dailydata/index.php>).

Discussion

The risk maps used to support these PRAs were all created by using short cuts and none of them utilised all components of the PRATIQUE DSSs for climatic suitability analysis (Eyre et al. 2012) and mapping areas at highest risk (Baker et al. 2012) although detailed investigations of the current distribution of the pest and its climate responses were generally carried out.

Based on the rationale for shortcuts described above, *P. austrocedrae* and *P. pityocampa* can be considered to represent, respectively, low and high priorities for pest risk mapping. For *P. austrocedrae*, distribution maps of juniper for the whole country and for areas important for nature conservation were considered to be sufficient to show the area of potential establishment outside parks and gardens and the endangered area for environmental impacts, whereas even the potential for establishment of *T. pityocampa* is highly uncertain. The risk mapping priorities for *D. suzukii* and *T. leucotreta* are intermediate. The area of potential establishment for both species was assessed with relatively simple methods based on climatic suitability analyses using, respectively, a simple phenology model and the difference between minimum and maximum winter temperatures with the distributions of the host crops primarily influencing the endangered areas and areas of highest risk.

The extent to which limited methods are appropriate to map risk is debatable because PRAs can only be validated when invasions occur. However, by ensuring that

the literature has been searched comprehensively to uncover, for example, all that is known about a pest's distribution, host range and climatic responses, greater reliance can be placed on the priority given and the methods used.

Short cuts and limited methods also generate greater uncertainty. Demonstrating uncertainty in maps remains a fundamental challenge (Venette et al. 2010) and so it is very important that pest risk analysts carefully document the uncertainties. For example, the *D. suzukii* PRA (EPPO 2011) noted that, although the 250 degree days above a base of 10°C used in Figure 2 is required for development from egg to adult, a simple division of the annual degree days to obtain a map of the number of generations possible in an area creates uncertainty because: (a) an additional period is usually required by insects before adults are ready to oviposit, (b) considerable individual variation can be expected with overlapping generations occurring and (c) the grid cells both summarise and interpolate climate measured at weather stations, many locations within each grid cell will have different temperature accumulations. In addition, although the higher the degree day accumulation above 10°C, the greater the number of generations expected, the species cannot tolerate high temperatures if humidity is low and, in the southern Mediterranean areas, the species may survive only in irrigated crops. While such uncertainties influence the area at highest risk and the endangered area for *D. suzukii* they do not fundamentally change the overall risk. For *T. pityocampa*, however, the uncertainties concerning winter solar radiation are so critical to the overwintering survival of PPM in southern England that the uncertainties do need further investigation.

Many other shortcuts are available in addition to the examples provided here. In fact the *D. suzukii* PRA also included a visual examination of the global Köppen-Geiger climate zones (Kottek et al. 2006), hardiness zones (Magarey et al. 2008) and day-degree (Baker 2002) maps to help with the assessment. Regional maps of environmental zones, e.g. for Europe (Metzger et al. 2005), may help because they provide greater resolution than global maps. Tools that match the climate at locations that would be novel to the pest with those in the area where the pest is present, irrespective of a pest's known climatic responses, can also be very useful. CLIMEX (Sutherst et al. 2007) provides an application for matching locations and regions that can exploit both weather station and gridded climatologies, e.g. CliMond (Kriticos et al. 2011).

Conclusions and further work

The PRATIQUE DSSs for mapping the suitability of the climate for pest risk analysis (Eyre et al. 2012) and mapping areas at highest risk (Baker et al. 2012) already provide advice and examples for (a) when to map and when not to map, (b) what climate suitability model to use, (c) where to find other relevant spatial data and (d) how to combine other relevant spatial data with climatic suitability to create maps of potential establishment. Some of the issues that require further work are: (i) the representation of uncertainty to pest risk managers, (ii) the incorporation of climate and land use

change in risk maps, (iii) linking maps of the area of highest risk with models of pest spread and impacts and (iv) exploring ways of mapping endangered areas. These challenges relate closely to the recommendations for improving pest risk maps identified by Venette et al. (2010).

This paper has focused on the additional challenges of identifying when pest risk mapping is a low and a high priority and relating this to an appropriate reduction or increase in the level of detail employed while ensuring that the uncertainties inherent in simplification are clearly demonstrated. We have shown that a number of approaches for simplifying the DSS and reducing the time taken to produce risk maps can be considered, e.g. (a) using previously published maps to help indicate risk, (b) deploying simpler models and (c) mapping key components for visual comparison without importing them all into a GIS, converting them to the same resolution and using GIS tools to highlight areas at high risk. However, the examples provided in this paper show that, to justify any shortcuts, it is always important to ensure that the literature is thoroughly searched for key information on, for example pest distribution, host/habitat range and climatic responses. In addition, any maps that have been generated from simplified approaches should be clearly documented so that the reader knows why these methods have been used and understands the uncertainties. The priorities for further research should also be indicated.

The future priorities for pest risk mapping DSSs include further testing and enhancements to address the challenges articulated in the roadmap provided by Venette et al. (2010) not only to assist pest risk mappers but also to guide policy makers when interpreting the maps produced. The identification of the situations that are priorities for detailed pest risk mapping with guidance on shortcuts relates closely to the increasing use of shorter PRA schemes that can be completed quickly, e.g. the Quick Scan PRA scheme of the Netherlands (Netherlands Plant Protection Service 2012), the Rapid PRA scheme of the UK (Fera 2012b) and the EPPO express PRA scheme (EPPO 2012).

Acknowledgements

We are very grateful to the OECD for sponsoring the workshop at which this paper was delivered. Richard Baker and Dominic Eyre thank Fera Plant Health for supporting our attendance. We acknowledge the work of many people that produced the work that is referred to in this paper. Their names are given below with their affiliation at the time of their contribution. PRATIQUE was funded by the European Union 7th Framework Programme Grant No. 212459 and the DSSs for climatic suitability and mapping the areas at highest risk were created by the authors of this paper in collaboration with Jan Benninga (LEI, The Netherlands), Johan Bremmer (LEI, The Netherlands), Maxime Dupin (INRA, France), Zhenya Ilieva (PPI, Bulgaria), Vojtech Jarosik (Institute of Botany, Czech Republic), Hella Kehlenbeck (JKI Germany), Darren Kriticos (CSIRO Australia), David Makowski (INRA, France), Jan Pergl

(Institute of Botany, Czech Republic), Philippe Reynaud (ANSES, France), Christelle Robinet (INRA France), Tarek Soliman (Wageningen University, The Netherlands), Wopke Van der Werf (Wageningen University, The Netherlands) and Susan Worner (University of Lincoln, New Zealand). The rapid PRA for *P. austrocedrae* was written by Joan Webber, Sarah Green, and Steven Hendry from Forest Research (UK) and reviewed by Claire Sansford (Fera, UK). The EPPO Expert Working Group for the PRA on *D. suzukii* consisted of: Richard Baker (Fera, UK), Peter Baufeld (JKI, Germany), Alberto Grassi (IASMA, Italy), Jose Maria Guitian Castrillon (TRAGSATEC, Spain), Martin Hauser (California Department of Agriculture, USA), Tracy Hueppelsheuser (British Columbia Ministry of Agriculture, Canada), Jon Knight (Imperial College, UK), Françoise Petter (EPPO), Philippe Reynaud (ANSES, France) and Rob Sunley (EPPO, France). The EPPO Expert Working Group for the PRA on *T. leucotreta* consisted of Richard Baker (Fera, UK), Peter Baufeld (JKI, Germany), Vaughan Hattingh (Citrus Research International, South Africa) Panagiotis Milonas (Benaki Phytopathological Institute, Greece), Françoise Petter (EPPO, France), Víctor Sarto i Monteyns (Servei de Sanitat Vegetal, Spain) and Marja van der Straten (Plant Protection Service, The Netherlands). The rapid PRA for *T. pityocampa* was produced by: Richard Baker, Helen Anderson, Sharon Matthews-Berry and Anastasia Korycinska from Fera (UK) with comments and corrections from John Morgan (Forestry Commission, UK) and Hugh Evans (Forest Research, UK) and assistance from Christelle Robinet (INRA, France). We acknowledge the UK Meteorological Office and the E-OBS dataset from the EU-FP6 project ENSEMBLES (<http://ensembles-eu.metoffice.com>) and the data providers in the ECA&D project (<http://eca.knmi.nl>) for the meteorological data. We are grateful for the comments made by Rob Venette and the anonymous reviewers in enhancing this paper.

References

- ABARES (2012) Multi-Criteria Analysis Shell for Spatial Decision Support (MCAS-S). Australian Bureau of Agricultural and Resource Economics and Sciences. <http://www.daff.gov.au/abares/data/mcass>
- Baker RHA (2002) Predicting the limits to the potential distribution of alien crop pests. In: Hallman GJ, Schwalbe CP (Eds) *Invasive Arthropods in Agriculture. Problems and Solutions*. Science Publishers Inc., Enfield, USA, 207–241.
- Baker RHA, Battisti A, Bremmer J, Kenis M, Mumford J, Petter F, Schrader G, Bacher S, De Barro P, Hulme PE, Karadjova O, Lansink AO, Pruvost O, Pysek P, Roques A, Baranchikov Y, Sun JH (2009) PRATIQUE: a research project to enhance pest risk analysis techniques in the European Union. EPPO Bulletin 39: 87–93. doi: 10.1111/j.1365-2338.2009.02246.x
- Baker RHA, Benninga J, Bremmer J, Brunel S, Dupin M, Eyre D, Ilieva Z, Jarosik V, Kehlenbeck H, Kriticos DJ, Makowski D, Pergl J, Reynaud P, Robinet C, Soliman T, Van der Werf W, Worner S (2011) Protocol for mapping endangered areas taking climate, climate change, bi-

- otic and abiotic factors, land use and economic impacts into account accessed via a hyperlink in a project web page and integrated into the web-based EPPO PRA scheme. PRATIQUE Deliverable 3.3. <https://secure.fera.defra.gov.uk/pratique/downloadItem.cfm?id=742>
- Baker RHA, Benninga J, Bremmer J, Brunel S, Dupin M, Eyre D, Ilieva Z, Jarosik V, Kehlenbeck H, Kriticos DJ, Makowski D, Pergl J, Reynaud P, Robinet C, Soliman T, Van der Werf W, Worner S (2012) A decision-support scheme for mapping endangered areas in pest risk analysis. EPPO Bulletin 42: 65–73. doi: 10.1111/j.1365-2338.2012.02545.x
- BSBI (2012) Botanical Society for the British Isles Maps Scheme. <http://www.bsbimaps.org.uk/atlas/main.php>
- Brunel S, Suffert M, Petter F, Baker R (2013) Interface between pest risk science and policy: the EPPO perspective. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models of invasive alien species in the food chain. NeoBiota 18: 9–23. doi: 10.3897/neobiota.18.4049
- Calabria G, Máca J, Bächli G, Serra L, Pascual M (2012) First records of the potential pest species *Drosophila suzukii* (Diptera: Drosophilidae) in Europe. Journal of Applied Entomology 136: 139–147. doi: 10.1111/j.1439-0418.2010.01583.x
- EPPO (2011) Pest risk analysis for *Drosophila suzukii*. http://www.eppo.int/QUARANTINE/Pest_Risk_Analysis/PRAdocs_insects/11-17189_PRA_record_Drosophila_suzukii_final%20.pdf
- EPPO (2012) 50th meeting of the Working Party on Phytosanitary Regulations. http://www.eppo.int/MEETINGS/2012_meetings/wp_pr_helsinki.htm
- Eyre D, Baker RHA, Brunel S, Dupin M, Jarosik V, Kriticos DJ, Makowski D, Pergl J, Reynaud P, Robinet C, Worner S (2012) Rating and mapping the suitability of the climate for pest risk analysis. EPPO Bulletin 42: 48–55. doi: 10.1111/j.1365-2338.2012.02549.x
- FAO (2004) Pest risk analysis for quarantine pests including analysis of environmental risks. International Standards for Phytosanitary Measures. Publication No. 11. Rev. 1. FAO, Rome.
- FAO (2012) Glossary of phytosanitary terms. International Standards for Phytosanitary Measures. Publication No. 5. FAO, Rome. https://www.ippc.int/file_uploaded/1336736415_ISPM_05_En_2012-05-07%28CPM-7%29.pdf
- Fera (2012a) Rapid pest risk analysis for *Thaumetopoea pityocampa*. Food and Environment Research Agency. <http://www.fera.defra.gov.uk/plants/plantHealth/pestsDiseases/pratTableNew.cfm>
- Fera (2012b) PRAs for consultation on pest risk management. Food and Environment Research Agency. <http://www.fera.defra.gov.uk/plants/plantHealth/pestsDiseases/pratTableNew.cfm>
- Forest Research (2012) Rapid assessment of the need for a detailed Pest Risk Analysis for *Phytophthora austrocedrae*. <http://www.forestry.gov.uk/forestry/INFD-8RAJZ3>
- Forestry Commission (2013) *Phytophthora austrocedrae*. <http://www.forestry.gov.uk/forestry/INFD-8RAJZ3>
- Griessinger D, Suffert M, Brunel S, Petter F (2012) CAPRA: the EPPO Computer Assisted PRA scheme. EPPO Bulletin 42: 42–47. doi: 10.1111/j.1365-2338.2012.02541.x
- Hauser M (2011) A historic account of the invasion of *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) in the continental United States, with remarks on their identification. Pest Management Science 67: 1352–1357. doi: 10.1002/ps.2265

- Joint Nature Conservation Committee (2007) Conservation Status Assessment for H5130 *Juniperus communis* formations on heaths or calcareous grasslands. Second Report by the UK under Article 17 on the implementation of the Habitats Directive from January 2001 to December 2006. JNCC. Peterborough. <http://jncc.defra.gov.uk/pdf/Article17/FCS2007-H5130-Final.pdf>
- Kehlenbeck H, Robinet C, van der Werf W, Kriticos D, Reynaud P, Baker R (2012) Modelling and mapping spread in pest risk analysis: a generic approach. EPPO Bulletin 42: 74–80. doi: 10.1111/j.1365-2338.2012.02550.x
- Kriticos DJ, Webber BL, Leriche A, Ota N, Macadam I, Bathols J, Scott JK (2011) Cli-Mond: global high resolution historical and future scenario climate surfaces for bioclimatic modelling. Methods in Ecology and Evolution 3: 53–64. doi: 10.1111/j.2041-210X.2011.00134.x
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of Köppen- Geiger climate classification updated. Meteorologische Zeitschrift 15: 259–263. doi: 10.1127/0941-2948/2006/0130
- Lee JC, Bruck DJ, Curry H, Edwards D, Haviland DR, Van Steenwykd RA, Yorgey BM (2011) The susceptibility of small fruits and cherries to the spotted-wing drosophila, *Drosophila suzukii*. Pest Management Science 67: 1358–1367. doi: 10.1002/ps.2225
- Lockton AJ (2012) Species account: *Juniperus communis*. Botanical Society of the British Isles. <http://sppaccounts.bsbi.org.uk/content/juniperus-communis-1>
- 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. doi: 10.1094/PDIS-91-4-0336
- Magarey RD, Borchert DM, Schlegel JW (2008) Global plant hardiness zones for phytosanitary risk analysis. Scientia Agricola 65: 54–59. doi: 10.1590/S0103-90162008000700009
- Magarey RD, Borchert DM, Engle JS, Colunga-Garcia M, Koch FH, Yemshanov D (2011) Risk maps for targeting exotic plant pest detection programs in the United States. EPPO Bulletin 41: 46–56. doi: 10.1111/j.1365-2338.2011.02437.x
- Metzger MJ, Bunce RGH, Jongman RHG, Mücher CA, Watkins JW (2005) A climatic stratification of the environment of Europe. Global Ecology and Biogeography 14: 549–563. doi: 10.1111/j.1466-822X.2005.00190.x
- Netherlands Plant Protection Service (2012) Evaluation of pest risks. <http://www.vwa.nl/onderwerpen/english/dossier/pest-risk-analysis/evaluation-of-pest-risks>
- New M, Lister D, Hulme M, Makin I (2002) A high-resolution data set of surface climate over global land areas. Climate Research 21: 1–25. doi: 10.3354/cr021001
- Pedigo LP, Hutchins SH, Higley LG (1986) Economic injury levels in theory and practice. Annual Review of Entomology 31: 341–368. doi: 10.1146/annurev.en.31.010186.002013
- Robinet C, Baier P, Pennerstorfer J, Schopf A, Roques A (2007) Modelling the effects of climate change on the potential feeding activity of *Thaumetopoea pityocampa* (Den & Schiff.) (Lep., Notodontidae) in France. Global Ecology and Biogeography 16: 460–471. doi: 10.1111/j.1466-8238.2006.00302.x

- Robinet C, Imbert C-E, Rousselet J, Sauvard D, Garcia J, Goussard F, Roques A (2011) Human-mediated long-distance jumps of the pine processionary moth in Europe. *Biological Invasions* 14: 1557–1569. doi: 10.1007/s10530-011-9979-9
- Schrader G, MacLeod A, Petter F, Baker RHA, Brunel S, Holt J, Leach AW, Mumford JD (2012) Consistency in pest risk analysis – how can it be achieved and what are the benefits? *EPPO Bulletin* 42: 3–12. doi: 10.1111/j.1365-2338.2012.02547.x
- Soliman T, Mourits MCM, Oude Lansink AGJM, van der Werf W (2012) Quantitative economic impact assessment of an invasive plant disease under uncertainty: A case study for potato spindle tuber viroid (PSTVd) invasion into the European Union. *Crop Protection* 40: 28–35. doi: 10.1016/j.cropro.2012.04.019
- Sutherst RW, Maywald GF, Kriticos D (2007) CLIMEX Version 3: Users Guide. Hearne Scientific Software Pty Ltd, Melbourne. <http://www.hearne.com.au/attachments/Climex-UserGuide3.pdf>
- UK Meteorological Office (2012a) UK mapped climate averages. <http://www.metoffice.gov.uk/climate/uk/averages/ukmapavge.html>
- UK Meteorological Office (2012b) Met Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations Data (1853-current). NCAS British Atmospheric Data Centre. http://badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dataent_ukmo-midas
- Venette RC, Kriticos DJ, Magarey RD, Koch FH, Baker RHA, Worner SP, Gomez Raboteaux NN, McKenney DW, Dobesberger EJ, Yemshanov D, De Barro PJ, Hutchison WD, Fowler G, Kalaris TM, Pedlar J (2010) Pest risk maps for invasive alien species: a roadmap for improvement. *Bioscience* 60: 349–362. doi: 10.1525/bio.2010.60.5.5

Practical guidelines for modelling post-entry spread in invasion ecology

Hazel R. Parry¹, Rohan J. Sadler^{2,3}, Darren J. Kriticos⁴

1 CSIRO Ecosystem Sciences, GPO Box 2583, EcoScience Precinct, Brisbane, QLD, 4001, Australia **2** Astron Environmental Services, 129 Royal Street, East Perth, Western Australia 6004 **3** School of Agricultural and Resource Economics, The University of Western Australia, 35 Stirling Highway, Crawley, 6009 **4** CSIRO Ecosystem Sciences and Biosecurity Flagship, GPO Box 1700, Canberra, ACT 2601, Australia

Corresponding author: Hazel R. Parry (hazel.parry@csiro.au)

Academic editor: W. VanderWerf | Received 13 November 2012 | Accepted 2 August 2013 | Published 13 September 2013

Citation: Parry HR, Sadler RJ, Kriticos DJ (2013) Practical guidelines for modelling post-entry spread in invasion ecology. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 41–66. doi: 10.3897/neobiota.18.4305

Abstract

In this article we review a variety of methods to enable understanding and modelling the spread of a pest or pathogen post-entry. Building upon our experience of multidisciplinary research in this area, we propose practical guidelines and a framework for model development, to help with the application of mathematical modelling in the field of invasion ecology for post-entry spread. We evaluate the pros and cons of a range of methods, including references to examples of the methods in practice. We also show how issues of data deficiency and uncertainty can be addressed. The aim is to provide guidance to the reader on the most suitable elements to include in a model of post-entry dispersal in a risk assessment, under differing circumstances. We identify both the strengths and weaknesses of different methods and their application as part of a holistic, multidisciplinary approach to biosecurity research.

Keywords

Biosecurity, Dispersal, Migration, Modelling, Post-entry spread

Introduction

Invasive species can have enormous economic and ecological impacts (Perrings et al. 2000, Pimentel 2011, Simberloff et al. 2005, Simberloff 2013). If we can assess the invasion threat early in the invasion process, we are likely to have more success in controlling the species, and suffer less impact than if we cannot. In general, the rate of spread of an invasive species will influence practical issues around our ability to control its spread and thus its ultimate impact. Targeted research to address the early, ‘post-entry’ stage of invasion is critical to inform management strategies and ultimately to improve biosecurity.

This article focuses on this ‘post-entry spread’ stage of the invasion process, specifically understanding dispersal processes and modelling the spread and establishment potential of a pest or pathogen once it has arrived into a region. We differentiate this from the population dynamics and dispersal of native species, as post-entry pest spread of non-native species has particular features that add to the modelling challenge. These include the requirement for rapid response, data paucity and high levels of uncertainty.

Whilst the majority of pest and pathogen entry today is largely due to anthropogenic pathways (Wilson et al. 2009), mainly from the transport of goods and commodities (Costello and McAusland 2003), once a pest has gained entry the mechanisms of spread can be multiple and diverse. The rate of spread will depend on a range of factors not just relating to the species’ ecology but also relating to host distributions and to potential dispersal vectors; not only human but animal and environmental (such as wind or ocean currents). Ecological factors and landscape context may influence the pest/pathogen, vector and host, either facilitating or inhibiting the dispersal of the species. Likewise, the success of individual dispersal events may be strongly influenced by low probability extreme meteorological events, or by human-induced or other environmental factors.

When integrated with field-based research and surveillance, dispersal models can help inform pest and pathogen outbreak management about a range of processes, such as the rate of spread of a pest (Gilbert and Liebhold 2010), which can lead to better surveillance strategies (Cacho et al. 2010, Demon et al. 2011, Epanchin-Niell et al. 2012), and more effective response strategies (Coutts et al. 2011). Models can also be used to inform policy-makers about the risks posed to target ecosystems (Rutherford et al. 1999), at both immediate and long-term time scales (Kriticos et al. 2003; 2013a). Similarly, integration of dispersal simulation models and economic models can help to inform the design of optimal management strategies (Bogich et al. 2008, Carrasco et al. 2009, Florec et al. 2013, Kriticos et al. 2013b). For example, models can be used to decide when and at what scale a management strategy should be implemented given the progression of an invasion, and to decide whether the costs will outweigh the benefits.

With such diversity of pathways, scales and complexity of dispersal processes for post-entry spread, and with such a wide range of possible applications, there is a parallel diversity of modelling methods. We aim to give an overview here to help guide modellers to select appropriate methods.

Background

Models of pest and pathogen spread post-entry largely occupy one of two categories of model: analytical methods (Hastings 1996, Kot et al. 1996, Neubert and Caswell 2000, Royama 1992) and mechanistic, process-based methods (Higgins and Richardson 1996, Jongejans et al. 2008). Analytical models have been used for many years to study dispersal in ecology, beginning with simple diffusion equations (Skellam 1951). An analytical model can be broadly defined as a deterministic mathematical expression. Such models seek to distil the complexity of a system or process into a single representation of its behaviour under given circumstances. They have the advantage that they tend to be more easily generalised than mechanistic models (Turchin 1998). They incorporate a range of techniques, in particular theoretical or empirical curve fitting models for dispersal kernels and other generalisations of the movement of organisms as a simplified physical process (e.g. travelling wave (Sharov and Liebhold 1998), matrix models (Parker 2000) and diffusion (Kot et al. 1996)). Analytical models have varying data requirements, depending on whether they are developed as purely abstract theoretical models or if they are phenomenological statistical models that are empirically derived. In the latter case data availability often becomes a big issue for modelling incursions (see following section). Such methods generally involve assumptions that include uniformity of the landscape and population, which mean they are simple to implement but can be highly abstract. Criticisms of these models are a lack of complexity and realism that can be key to studying processes such as long-distance dispersal and the influence of landscape heterogeneity. Moreover, long-distance dispersal events are often caused by different mechanisms to short distance dispersal and are highly significant drivers of accelerated population spread (Liebhold and Tobin 2008).

To explore the long distance connectivity of populations, network models and metapopulation models have also been applied to invasion ecology in recent times (Chadès et al. 2011, Drake and Mandrak 2010, Facon and David 2006, Paini and Yemshanov 2012). Whilst these also have the advantage of simplifying complex processes, equally they make their own assumptions about the uniformity and ‘patchiness’ of the landscape.

Mechanistic, process-based simulation models are a more recent development for modelling spread post-entry (Turchin 1998), enabled in part by the growing power of computing to support large, complex models. Such approaches to dispersal modelling align with ‘ballistic’ simulations or in physics termed ‘Lagrangian’ models – where individual pathways are traced as they move according to a set of stochastic or behavioural rules (e.g. individuals influenced by wind trajectories). Such models tend to have greater flexibility across spatial scales, and therefore can more easily encompass both short and long distance dispersal events. Consequently, individual-based models (Grimm and Railsback 2005), cellular automata (Travis and Dytham 2002) and trajectory models (Chapman et al. 2010, Nathan et al. 2005) have become part of the ecological modeller’s toolkit over the last few years, although there are relatively few

examples of the application of these methods to dispersal modelling for post-entry spread (e.g. Guichard et al. 2012, Kanarek et al. 2012).

It is also possible and can be advantageous for a dispersal model to contain both analytical and mechanistic components (e.g. Nathan et al. 2011). One example is WALD (Katul et al. 2005), which is used to estimate long distance dispersal kernels of wind-dispersed seeds and their escape probability from the plant canopy. A computationally intensive trajectory model that incorporates the effects of canopy turbulence was used to derive an expression for an analytical model, therefore retaining the mechanisms but giving the advantage of analytical simplicity (essentially an inverse Gaussian distribution). More broadly, bringing together the simplicity of an analytical, phenomenological method with mechanistic understanding of processes can be very powerful (e.g. Pitt et al. 2011).

Multiple dispersal vectors add extra layers of complexity (Buckley et al. 2006, Pitt et al. 2009). Many species have multiple dispersal pathways and these can be considered by the model(s), using an integrated multi-modelling method (Harwood et al. 2009).

In addition, species niche models can inform post-entry spread in multiple ways. Firstly, they can inform the total area that can potentially be invaded. This information can define the spatial bounds of the spread modelling, i.e., the model ‘universe’, for both simulation and analytical spread models. Alternatively, a niche model can be used to differentiate between different components of a heterogeneous landscape over which a species may spread, and this can be used by spatially-explicit dynamic dispersal models (e.g., Pitt et al. 2011).

When considering how best to apply these models, understanding the ecology and landscape factors relevant to the population dynamic and dispersal of a pest or pathogen species is critical. Often, not enough consideration is given to an organism’s ecology and behaviour prior to developing a dispersal model, where population dynamics models are commonly separated from dispersal simulation. However, biological processes operating at different spatial and temporal scales are key drivers in the dispersal process, and ideally should be taken into account explicitly.

In selecting a model, there are also important characteristics to consider, such as the *sensitivity* of the model (the proportion of known spatio-temporal dispersal events modelled correctly) *versus* the *specificity* of the model (the proportion of unoccupied sites that are modelled correctly) (Fielding and Bell 1997, Pitt et al. 2011). Where spread models combine highly specific model realisations to create a probability surface for occupancy, they inevitably become less specific through time, eroding their usefulness for addressing long-term strategic questions (Pitt et al. 2011). A good example of the sensitivity-biased effects of applying a stochastic mechanistic modelling method to long-term dispersal scenarios is Robinet et al. (2009). In this paper, the spread of the pinewood nematode was simulated over 23 years in China. A probability surface of nematode presence was generated from a combination of 300 replicate simulations. The fit of the model was assessed by comparing how many of the known locations fell into cells with a positive modelled probability. This commonly applied method ignores the model specificity (the number of cells that had a positive modelled probability, but did not include any

reported infestations). As a guide for surveillance activities, poor model specificity could lead to much wasted effort, and for pest risk, an over-estimate of the potential impacts of the pest due to inappropriately high rates of spread. Therefore there is a need to critically consider this effect when developing a model of post-entry dispersal (Fletcher and Westcott 2013), perhaps limiting mechanistic models to short-term tactical applications such as informing regional pest management plans, including activities such as surveillance, eradication and containment strategies, and using far simpler spread models for strategic applications such as pest risk modelling (e.g. Kriticos et al. 2013b).

The post-entry spread modelling framework

Defining biosecurity objectives

The rate of spread of a pest or pathogen can affect the present value of its future economic and ecological impacts, taking into account the economic discount rate; all else being equal, a slower-spreading pest/pathogen is thought to have less potential future impact than a faster-spreading one. However, for terrestrial plants in particular, there may be a deceptive time lag between the arrival of the pest and the point at which the rate of spread begins to accelerate (Mack et al. 2000). Thus, shortly after establishment it can be difficult to discern a potential invasive from a non-invasive species. This may hamper our ability to model such cases accurately unless the potential drivers of both the lag phase and subsequent growth phase of spread are known. The rate of spread of a pest can also influence practical issues around our ability to control its spread (not necessarily a linear relationship), and the communication tactics employed (e.g. emphasising detection and slowing the spread, versus advising land managers about methods to control the pest once it arrives in an area) (Sharov and Liebhold 1998).

The International Standards for Phytosanitary Measures (FAO 2006) highlight various factors that are important to the estimation of the spread potential of an organism after establishment. These include the need for reliable biological information on pest occurrence, which can then be compared with the outbreak situation. Key considerations include:

- suitability of the natural and/or managed environment for natural spread of the pest,
- movement with commodities or conveyances,
- intended use of the commodity,
- potential vectors of the pest in the outbreak area,
- potential natural enemies of the pest in the outbreak area.

In this regard, we seek to estimate the potential extent of the endangered area, as well as the likely rate at which that area might become occupied by the organism. In the early stages of response it is important to assess the factors above as rapidly as possible, along with the route of introduction, the mechanisms of subsequent movement

and the shape of the natural dispersal kernel. Some factors will be easier to assess than others. While the potential extent can be estimated using niche modelling methods based on the organism's overseas distribution and where available knowledge of its ecology, simulating the organism's rate of spread relies on estimated spread rates, of which our knowledge is often poor. For example, use of Ripley's K-function or an O-ring analysis with available data (Wiegand and Moloney 2004) allows rapid estimation of the likely points of introduction and spatial clustering by statistically analysing and describing aggregation or dispersion patterns up to or at a given distance from a source. However, many of the other parameters required for a full assessment of spread potential may not be estimated readily until after several months of research.

Post-entry spread models: from the conceptual to the mathematical

A framework is suggested for post-entry dispersal modelling (Fig. 1). We expand on the key aspects of this framework in the following sections. Important to this process are clearly defined biosecurity objectives and scale informing the conceptual model (1), with an awareness of the constraints (such as time and the value of the problem in terms of pest/pathogen impact). Two primary issues are faced when modelling post-entry spread: obtaining data for model parameterisation and the difficulty of modelling multiple dispersal pathways (Pitt et al. 2009). Data availability can be a limiting factor in post-entry dispersal modelling, thus a consideration of what data is available is critical at the conceptual stage. Data availability may constrain how the model can be calibrated (3) or evaluated once the model is developed, which will affect the reliability of the model results (4). In addition, at the model refinement stage (3 and 4), the modeller may also include other methods with which to refine a model, such as Bayesian learning, and also validate the model, if appropriate data is available. In addition, an estimation of model uncertainty is an important basis for reliable decision making.

In the model formulation (2), a consideration of *scale* and *complexity* is paramount. How complex can the model be, given the availability of data and knowledge of the system, and how complex does the model need to be to address the salient questions? In general the complexity of a model is determined by the model scope and purpose, and the complexity of the study system. However, in rapid response situations, the inevitable lack of data means that in general it is best to construct simple (perhaps over-simplified) models rather than complex models (Jørgensen and Bendoricchio 2001). This may mean that species-specific models require rapid construction or that general model (e.g. traits-based or 'meta-models') may be applied in a specific incursion context (Saltelli et al. 2008). An advantage of simpler models is their more rapid generalisation to future contexts defined by new invasive species and landscapes, though it is important that such models balance generality with a need to include important processes at a sufficient level of mechanistic realism (Renton et al. 2011, Savage et al. in press).

As more data becomes available, model complexity and specificity can be increased. When selecting a modelling method, we suggest that modellers should con-

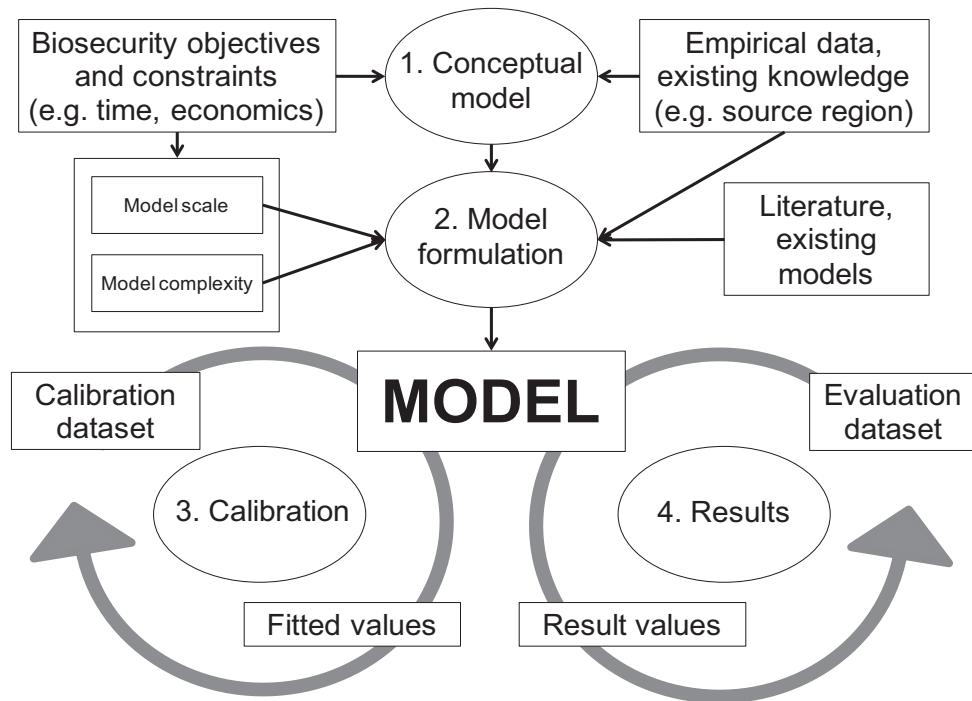


Figure 1. A framework for the model building process, when two data sets are available – one for fitting and one for evaluating the model (after Guisan and Zimmermann 2000).

sider a) the minimum level of model complexity required to address the pressing and foreseeable management and research questions, and b) the maximum level of model complexity that can be supported by the available knowledge and resources. Where $a < b$, the modeller has the option of choosing to build an elaborate model, perhaps capable of addressing unthought-of questions. Where $a > b$ there is an information deficit and decision-makers expectations and confidence in the model results may need to be managed carefully. For pre-border risk assessments, there is latent demand for spatially-explicit spread models that are combined with impacts. Unfortunately, the initialisation of such models is a critically sensitive factor. Prior to an incursion and establishment of a pest or pathogen, the starting point for the spread model is unknown, and unknowable, a situation similar to that of the state of Schrödinger's Cat prior to opening the box.

The importance of scale

Temporal and spatial scale has an important role in the modelling process. Models for invasion post-entry pest spread most often need to be spatially-explicit, as landscape structure can impact on the invasion process significantly (With 2002) and policy-

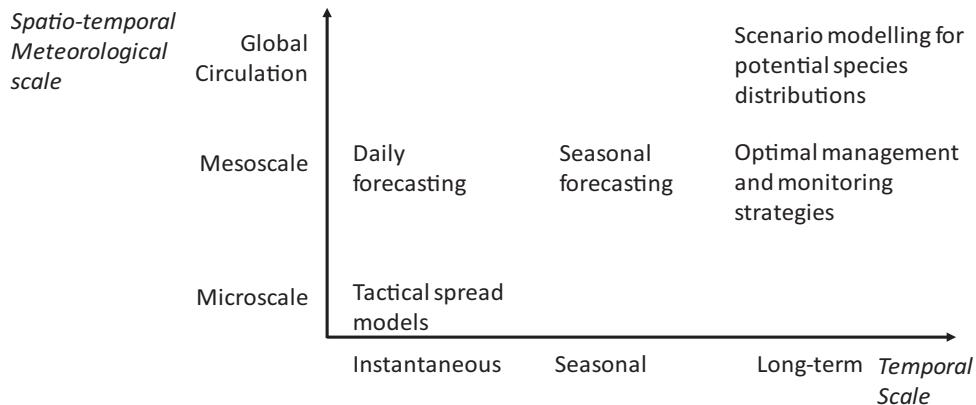


Figure 2. Pest and pathogen modelling foci at different spatio-temporal scales.

makers generally consider both pest-led and site-led management strategies. This allows models to inform spatial contingency planning to control or manage an outbreak. Some policy relevant applications outlined in the introduction are more relevant at particular landscape scales than others, or may be answered in different ways depending on the scale of the model. For example, there are five different kinds of model that are developed for post-entry spread of pests or pathogens to address policy relevant issues: tactical spread models, daily forecasting, seasonal forecasting, optimal management and monitoring strategies, and scenario modelling for future species distributions. The different focuses of the models result in them operating at different spatial-temporal scales (Fig. 2). Models that operate on a ‘short-term’ timescale, i.e. days to months, tend to also focus at a local spatial scale close to an outbreak, to consider issues of tactical spread and daily or seasonal forecasting. ‘Long-term’ models, i.e. operating across years to decades, tend to operate at much larger spatial scales to consider future species distributions and long-term management or monitoring strategies.

Although operating at different spatio-temporal scales, all of these models are likely to be required as soon as possible in a biological invasion. For example, long-term pest risk assessments are critical to help evaluate the suitable level of response to the incursion, e.g. through an economic analysis (e.g. Bogich et al. 2008, Carrasco et al. 2009, Kriticos et al. 2013b). Scenario models may also be constructed that allow for the user to explore potential invasion pathways, rate of spread and locations at risk (e.g. Harwood et al. 2009). These all require a certain capacity to simulate the movement and timing of pest outbreaks following the initial establishment.

A methodological roadmap

To summarise the broad range of methods that are available to modellers, we have identified important attributes of each of the model types that are commonly used to simulate post-entry spread (Table 1). For each of these methods, we highlight the common model

Table 1. Summary of model types and characteristics commonly used in post-entry pest and pathogen modelling, including examples and key references.

Model Type	Spatially implicit	Dispersal Kernels	Individual-based models	Cellular Automata	Gaussian Plumes	Trajectory models	Network models and Metapopulation models	Potential distribution
Common model focus (see also Fig. 2)	Tactical spread; Daily forecasting	Tactical spread; Daily forecasting	Seasonal forecasting	Tactical spread; Daily forecasting	Seasonal forecasting; Scenario modelling for future distributions	Seasonal forecasting; Scenario modelling for future distributions	Seasonal forecasting; Scenario modelling for future distributions	Seasonal forecasting; Potential distribution, identifying the assets at risk; providing a forcing function for the rate of spread across heterogeneous landscapes; Scenario modelling for future distributions
Common model spatial scale (micro, meso, global circulation)	Mesoscale	Microscale; Mesoscale	Microscale; Mesoscale	Mesoscale	Mesoscale; Global circulation	Mesoscale; Global circulation	Mesoscale; Global circulation	Mesoscale; Global circulation
Common model temporal scale (instantaneous, seasonal, long-term)	Seasonal; long-term	Instantaneous	Instantaneous; Seasonal	Seasonal	Seasonal; long-term	Seasonal; long-term	Seasonal; long-term	Seasonal; long-term
Category (analytical or mechanistic)	Analytical	Analytical	Mechanistic	Mechanistic	Analytical	Mechanistic	Analytical	Analytical (majority), but some can be mechanistic or semi-mechanistic.
General pest / pathogen characteristics	Passive movement; Single dispersal event	Passive movement; Single dispersal event	Any mobile organism	Any mobile organism	Passive movement; Single dispersal event	Any mobile organism	Population contained within a clearly identifiable area/habitat.	Any organism. Works best with sessile organisms, though some models can accommodate mobile organisms.
Common data requirements	Pest source; Dispersal rate; Population density	Population density; Dispersal distance; Behavioural history; Dispersal rules (including dispersal); Pest source; Wind speed and direction; Pest and direction; Pest source.	Individual life-history; Behavioural history; Dispersal rules (including dispersal); Pest source; Landscape data (e.g. land use, habitat suitability etc).	Dispersal distance; Dispersal rate; Wind speed and direction; Pest source; Pest population dynamics; Population source.	Pest source; Dispersal rate; Wind speed and direction; Pest source; Pest population dynamics; Population source.	Habitat patches; Multi-level wind field	Habitat patches; Population dynamics; Population density; Dispersal rate; Pest dispersal (between patches); 'connectivity' and 'travel cost' between patches.	Well known pest distribution at least in native range (presence and absence) and ideally some information on introduced range; constraints on pest survival and population growth

Model Type	Spatially implicit	Dispersal Kernels	Individual-based models	Cellular Automata	Gaussian Plumes	Trajectory models	Network models and Metapopulation models	Potential distribution models
Invasion ecology examples	Waage et al. (2005)	Carasco et al. (2010), García Advea et al. (2012), Harwood et al. (2011), Lindstrom et al. (2007), Nehrbass et al. (2011), Savage et al. (2011)	Higgins et al. (1996), Higgins and Richardson (1998), Nehrbass et al. (2007), Nehrbass et al. (2011), Murphy et al. (2008), Rutherford et al. (1999)	Kawasaki et al. (2006), Merow et al. (2011), van Dorp et al. (1997)	Monty et al. (2008), Skelley et al. (2010)	Deveson et al. (2011), Drake and Mandrak (2010), Soroka (2010), Facon and David (2006)	Chadès et al. (2011), Hopkins and Hopkins (2010), Facón and David (2006)	Kriticos et al. (2003), Yonow and Sutherst (1998);
Key References	Shigesada and Kawasaki (1997)	Greene and Calogeropoulos (2002), Kor et al. (1996), Skellam (1951)	Grimm and Railsback (2005)	Travis and Dytham (2002), von Neumann (1951), Wolfram (1983)	Overcamp (1976) Scott and Achtemeier (1987), Nathan et al. (2011)	Hanski (1999), Moslonka-Lefebvre et al. (2005), Kunz et al. (2008)	Elith and Leathwick (2009), Elith et al. (2010), Kriticos and Randall (2001), Sutherland and Bourne (2009), Webber et al. (2011)	Elith and Leathwick (2009), Elith et al. (2010), Kriticos and Randall (2001), Sutherland and Bourne (2009), Webber et al. (2011)
Advantage	Minimal data requirements.	Minimal data requirements.	Accounts for environmental heterogeneity; Emergence; Flexibility; Scale free.	Accounts for environmental heterogeneity; Less computationally and complex; data intensive than fully individual-based models.	An analytical simplification of atmospheric or oceanic processes; Can account for minimal data requirements.	Incorporates atmospheric or oceanic processes; Can account for landscape effects at multiple scales.	Relatively simple; Allows examination of important processes including connectivity and long-term risks;	Long-term risks; incorporates environmental change; large scale.
Disadvantage	Highly simplistic; assumes uniform landscape; Relatively simplistic	Often assumes uniform landscape; Relatively simplistic	Complexity; data intensive; Species specific	Strong influence of grid cell size and shape on dispersal; Relatively simplistic treatment of dispersal; May not be biologically realistic.	Assumes uniform landscape; data intensive	Complexity; data intensive	Assumes clearly defined habitat patches; complete knowledge of 'empty' and 'occupied' sites; Relatively simplistic treatment of dispersal.	Ignores evolutionary change; Scale specific.

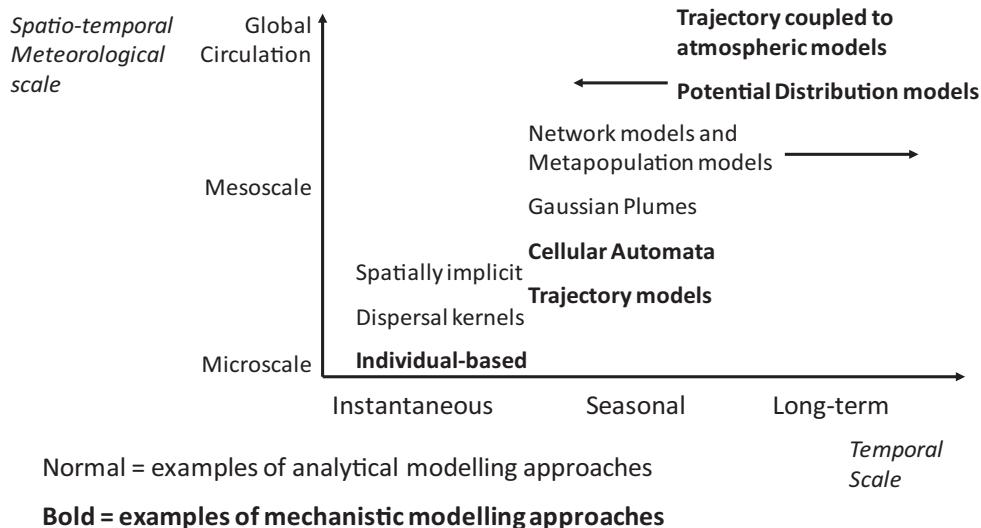


Figure 3. Examples of dispersal modelling techniques employed at different spatio-temporal scales.

focus and application, with references to some key examples in the literature. We identify the common data requirements, and highlight the overall advantages and disadvantages of each method. We also categorise the models according to their most appropriate temporal and spatial scale of use (although we acknowledge there is some potential overlap between our categories and that our references may refer to more than one scale or approach).

By understanding the scale at which policy questions are formulated (Fig. 2), we can align the spatio-temporal scale at which particular modelling techniques are best applied (Fig. 3) to identify which modelling methods may be best to use for particular policy questions (Table 1). However, it should be noted that in many cases it is necessary to examine an incursion event at multiple spatial and temporal scales and there can be significant advantages in doing so, such as an increased understanding of the invasion process and accounting for non-equilibrium of the species with the environment (Jones et al. 2010). This means that the modeller may need to select a flexible modelling approach that can span multiple spatial scales (see Table 1), or it may be necessary to develop multiple, possibly integrated models to address the range of dispersal pathways or policy questions that are posed. To further illustrate the pathway the modeller may take to arrive at using a particular modelling approach (or approaches) to address a particular problem, we have condensed the above to a flow-diagram (Fig. 4). This is intended as a further guide and illustration of the concepts in this paper. Constraints dictate the type of model and level of complexity that can be achieved, in relation to a biosecurity objective. In particular, the complexity of a model will be constrained by the available knowledge about the organism and its behaviour, that may lead to assumptions about the organism. Constraints may also relate to the level of complexity and capacity for model development. It may be that to achieve an appropriate model, constraints must be overcome as there is no other option.

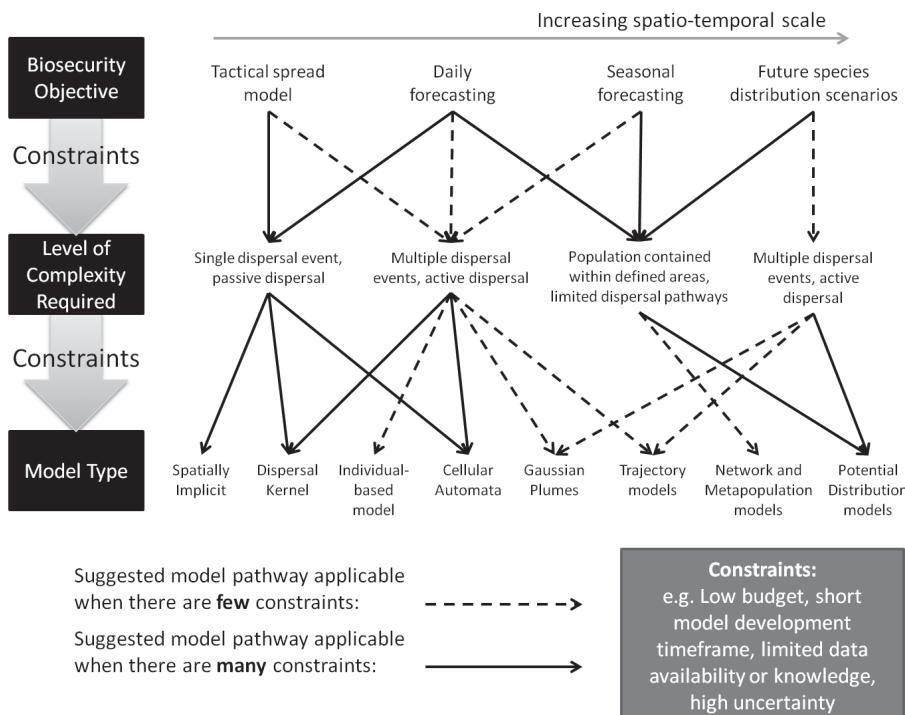


Figure 4. Flow diagram to illustrate the modelling process with concepts from this paper.

To explore the flow diagram, first consider the objective of the modelling exercise, the spatial temporal scale and consider the existing knowledge about the organism (as indicated above); this defines the level of model complexity (with constraints). For example, if the objective is to make a tactical spread model very quickly, about an organism that little is known about, then this means there are many constraints on the approach that can be taken (i.e. time and knowledge). Due to this constraint, the level of complexity is best viewed as a single dispersal event with passive dispersal (i.e. solid line, Fig 4). At this level of complexity, the options available in this case (Spatially Implicit, Dispersal Kernel or Cellular Automata, Fig. 4) are suitable even under many constraints (solid line, Fig. 4), so any of these could be applied, with the final decision based on the appropriate spatio-temporal scale and to some extent the personal preference of the modeller (arrow at top, Fig. 4).

To give a more complex example, the objective is to make a large-scale seasonal pest forecast model about an organism that has multiple modes of dispersal, both active and passive ranging across multiple habitats/pathways. As this objective relates to a complex model including multiple dispersal events and active dispersal, then a model of this complexity is only possible to construct if there are few constraints (i.e. dash line). The model development requires a certain level of existing knowledge about the organism's behaviour and perhaps a certain financial budget or amount of time to gather the information and develop the model. Given that the constraints are surmountable and it is possible to acquire the knowledge within the timeframe, then

different model types might be chosen, again relating to further constraints on model complexity/development such as budget/time: (1) if there are many constraints at this point the suggestion is the use of dispersal kernels or cellular automata – which simplify the known complexity of the dispersal events and mechanisms, or (2) if there are few constraints then a mechanistic approach may be taken such as individual-based modelling, gaussian plumes or trajectory models, all of which can better represent the complexity of the dispersal mechanisms. The other option for seasonal pest forecasting, if the first constraint cannot be met (i.e. the modeller is required to assume highly simplified behaviour such as limited dispersal pathways within defined areas), then the modeller can make the assumption of a more limited mode of dispersal that allows for such constraints. This leads to a different approach where the preferred option (if there are further constraints relating to e.g. model development time and budget) would be potential distribution models; however if a more dynamic approach is feasible by fewer constraints at this point (e.g. as there is good data availability about movement pathways) then network models/metapopulation models may be more appropriate.

Data availability

The importance of integrating field-based research and surveillance efforts with models as part of an ongoing multidisciplinary research effort continues to be highlighted in the literature (Restif et al. 2012). Ideally, a library of observed spread rates can provide valuable parameterisation for models, whilst at the same time models may inform ongoing surveillance efforts (e.g. Leighton et al. 2012, Leskinen et al. 2011, Fletcher and Westcott 2013). However, in practice good data are rarely available for post-entry spread modelling. Surveillance efforts may be *ad hoc*, and therefore not provide full coverage of the range and dispersal rate of the pest or pathogen as the invasion front moves. This is especially the case if the intrinsic probability of detecting an organism when present is low, given the existing surveillance technologies. Indeed, it is the estimated capacity for dispersal that will greatly influence the modelled rate of spread of the organism. For example, leptokurtic dispersal kernels (i.e. fat tailed compared to a normal distribution) lead to accelerating rates of population spread (Shigesada et al. 1995). While the extreme “fat tailed” dispersal events can have the largest influence on the overall behaviour of a dispersal model, it is these extreme events that are the most difficult to observe, and hence to estimate their prevalence. Even if good spread rate data are available on the characteristics of a species in another invaded range, this may not transfer into the context of a new region due to differences in natural and anthropogenic conditions. Models must therefore be constructed with an awareness of the shortcomings of data availability and the impact this will have on the model results, including presence-only data, bias to particular regions, missing life-history parameters and habitat suitability information.

Dispersal data are amongst the most difficult to collect and interpret. *Post-hoc* inferential methods relying on date-stamped geographical location records for invasions may be biased, incomplete and collected at a scale that is poorly suited for spread

modelling (Pitt et al. 2011), and there are few published examples of validated models derived from this source. Direct observations of spread rates are typically confounded by multiple potential sources of dispersers. Battisti et al. (2006) observed and measured an unusually rapid range expansion of winter pine processionary moth in its native range related to climate change, which was subsequently used to inform a simple spread simulation model for the invasion of New Zealand (Kriticos et al. 2013a).

Observations of the movement of an individual may have little informative value for the spread of a population. Spread rates for a species may vary greatly in relation to the potential movement of individuals, depending upon the suitability of the environment for population establishment and growth (Waage et al. 2005). Finally, there may be multiple dispersal pathways and therefore spread rates for a single organism: natural means of spread (e.g. wind dispersal) are often combined with long-distance transportation by humans or other animals (Harwood et al. 2009, 2011).

A key data requirement common for many models is to identify the incursion source. This underlines the importance of studies and models to identify entry points. However, even this may not be readily identifiable, and modellers must often work with partial information on an already spreading population without knowing the precise origin. Next, information on dispersal, such as movement rates, distances and directions are required. In more mechanistic methods, population dynamics and life-history parameters are required in order to simulate how individual dispersal events arise from a population. Habitat suitability and landscape data are also highly important in mechanistic, spatially-explicit simulations. A mechanistic method allows us to include important landscape interactions, such as foraging for food and breeding hosts, which can be critical factors of spread. This is one of the major advantages of a mechanistic method over an analytical one, as we are rarely able to adequately use an analytical approach to include the interaction of the organism with the landscape.

Ongoing monitoring and data acquisition is one solution to providing modelling support for decision-making in the face of knowledge scarcity. Existing models may be updated by calibration to fit new data as it is acquired, for example using methods such as a Kalman filter (most commonly used to update state-space equation model estimations with newly observed values, e.g. Hlasny 2011), allowing for more accurate short-term projections. However, the utility of the calibrated model estimates for a long term strategy is potentially compromised, as the underlying mechanism of population growth and dispersal can be mis-specified (e.g. Hooten and Wikle 2008). Thus, model reformulation and/or re-estimation is generally the most robust means to incorporate new data when the new data justifies it (Fig. 1).

Integrating existing knowledge and handling uncertainty

Knowledge gaps may relate to either a gap in knowledge of how a process is understood and therefore modelled (i.e. model uncertainty), or the uncertainty with which we can estimate the true value of a model parameter (parametric uncertainty). If the

knowledge of a critical process is incomplete, it is prudent to be cautious, and to be wary of management imperatives derived from regression-based patterns. The method of multiple competing hypotheses (Chamberlin 1890, Hilborn and Mangel 1997) is starting to gain popular acceptance as a basis for both studying and communicating deep uncertainty in areas as diverse as ecology and intelligence (Beven et al. 2005). An adaptive management, monitoring and modelling framework (A3MF) may be an appropriate method to adopt. In A3MF a model is iteratively updated as new knowledge or data is acquired that shows the model fails to represent the ecological process well (Holling 1978). Potential also exists within A3MF to employ different management strategies in different regions or periods of time to observe the response of the invasive organism to the different strategies and contexts, thereby accelerating our acquisition of knowledge about the organism and its management. However, A3MF requires long-term investment by a team of experts and managers over a time scale akin to the time scales of the invasion process, and the lagged impacts the invasion may have on the invaded agricultural or ecological system. This weakness of A3MF in its fullest sense is one of the reasons why simple, readily applied models have such broad appeal.

Parameter uncertainty, as a knowledge gap, is a function of data paucity and the availability of statistical methods. Model complexity also contributes to parameter uncertainty. On the one hand, highly complex models may contain so many parameters that not all may be known adequately, but on the other hand models that are very simple often contain parameters that are hard to estimate. Commonly, individual parameters are estimated through monitoring or experimental data targeted towards those parameters. These parameter estimates are then used in the model. If uncertainty in the estimates is quantified then the parameter uncertainty can be fed through the model to provide an estimate of parameter sensitivity. Other sources of uncertainty can also be incorporated into models through developing Bayesian posterior confidence intervals, such as measurement error or errors assigned to *ad hoc* parameter values (Higgins et al. 2003). In general, Bayesian methods have improved greatly with recent advances in computing, and can support a direct fitting of the model to the data, rather than a parameter plug-in approach. Hierarchical Bayesian methods of inference enable population dispersal models to be fitted to the data (Hooten and Wikle 2008, Royle et al. 2007). In lieu of a direct model-fitting procedure such as Hierarchical Bayes then the *ad hoc* ‘plug-in’ methods of model calibration are required, which may include:

1. garnering parameter values from analyses of the existing literature; or
2. minimising some measure of discrepancy between model output and the limited set of observations available, and which includes Approximate Bayesian Computation (ABC; Marjoram et al. 2003) and the inverse model problem.

Simulation is perhaps the best way to assign ‘prediction’ error or intervals to deterministic models, given uncertain starting conditions of the pest/pathogen population. Posterior prediction intervals can also be derived for stochastic models through cross-validation, and more generally through the use of independent test and training data sets. Generating

prediction intervals to be tested against new data sets also falls under the rubric of model validation (e.g. Higgins et al. 2001), which should also include logical tests for the “reasonableness” of model results. If model uncertainty of various management options on the end point of the invasion can be specified then a measure of policy or management activity risk can be developed, which may help determine an optimal risk mitigation strategy.

Common to all dynamic models is a temporal limit in quantifying model error. In this case an error is associated with a single time step, and in iteratively running a model then the error is compounded. The consequence of this compounding error is that long term utility of any dispersal model is dogged by severe and growing uncertainty. Two options are then available: (i) continual updating of results by resetting the model's initial conditions to the current conditions (e.g., the Kalman Filter process); or (ii) applying a decision method developed for severe uncertainty. Continual updating is consistent with both A3MF and Bayesian model updating, or ‘learning’: as new data arrive then our understanding of the processes, our ability to predict system processes, or belief in our model should also improve. However, continual updating requires ongoing monitoring to feed the model any change in system state as it occurs. Continual updating is most appropriate for developing tactical management responses to invasions, but does nothing to address the inability of these models to address strategic questions in a timely manner.

In contrast, decision making under severe uncertainty is common for long-term strategy development, or where continual updating is a cost-prohibitive option. Several analytical decision frameworks have been developed for dealing with severe uncertainty, with the two most popular being robust optimisation (RO) (Ben-Tal et al. 2009, Hansen and Sargent 2007) and info-gap theory (IGT) (Yakov 2006). The key difference between the two methods is that IGT provides a robust decision only in the local neighbourhood of the best guess parameter value for a model, whereas RO provides a solution that is robust over the entire range of parameter values to worst case scenarios (Sniedovich 2010). Neither framework handles a multivariate decision and parameter space well. A conservative strategy is to limit decision frameworks under severe uncertainty to those few key parameters that contribute most to the variability in model output, as identified through a sensitivity analysis.

Discussion

There is no single recipe for constructing a model of post-entry spread, due the diversity of policy applications, ecological and landscape contexts, temporal and spatial scales and possible techniques to employ. We have attempted to present some practical guidelines on how to approach model framing and construction for post-entry spread in invasion ecology by identifying what method may be most suitable to apply to particular policy questions, at what spatial and temporal scale, given the available data and knowledge. In recent years, we have seen the evolution of more process-based, mechanistic models that attempt to capture system dynamics and complexity. This trend has been supported (and perhaps encouraged) by the availability of suitable computer plat-

forms capable of processing the immense amount of information required to simulate these processes, as well as the availability of suitable covariate data.

The need for a more rapid response in outbreak situations has resulted in the recent development of fine-scale dispersal models designed to forecast and backcast spread for surveillance and response activities (Guichard et al. 2012) and generic models, such as a General Model of Biological Invasions (GMBI) (Renton et al. 2011, Savage et al. in press), Modular Dispersal in GIS (MDiG) (Pitt et al. 2009, 2011), demoniche (Nenzén et al. 2012) and a model suite for Pest Risk Analysis (Robinet et al. 2012). In the future, we anticipate modelling methods will continue to improve our ability to incorporate complex spatial and temporal dynamics, such as highly mechanistic models of wind dispersal. For example, recent research has simulated seed dispersal using a ballistic method coupled with large-eddy simulations incorporating turbulent airflow (Nathan et al. 2011). As sophisticated, multi-level wind circulation models are improved and made more accessible for a wider range of applications (e.g. NCEP/NCAR reanalysis data (NOAA 2011)), the opportunity to couple mechanistic dispersal models with process-based population dynamics models becomes apparent (Parry et al. 2011).

However, even when armed with limitless computing power and knowledge of a species' dispersal ecology we cannot forecast far into the future with high precision. We should be wary therefore of applying increasingly sophisticated mechanistic models and running them for long-term forecasts; the results may appear to have a fine resolution, but this should not be confused with reality – in such instances an analytical approach may be preferable, where fewer variables, constrained behaviour and obvious lack of precision make more explicit the model uncertainties and inaccuracies. Overall, there is great value in combining modelling methods; indeed it is likely to be necessary as the multi-dimensionality of the problem of post-entry pest spread will often require an integrated, multi-model, multi-scale approach, aligned with an empirical surveillance programme.

The most pressing limitations to applying spread modelling to post-entry invasion ecology are clearly not methodological. Modellers are spoilt for choice. The biggest constraints concern our knowledge of the rates of spread of organisms in novel landscapes at fine spatial and temporal scales, as well as across the time course of invasions. A clear challenge here is the cost of monitoring the spread of invasive organisms, which typically sees a rapid decline in interest once an organism stops being an eradication target. Options for overcoming this problem include placing more emphasis on the collection of time-stamped location data for invasive species, “crowd-sourcing” initiatives, and the development of a rich library of spread rate data for different organisms.

Acknowledgements

This work was primarily completed during the course of a post-doctoral fellowship at CSIRO, supported by the Cooperative Research Centre for Plant Biosecurity. The authors would like to thank the International Pest Risk Modelling Workgroup <http://www.pestrisk.org/> for their support and helpful discussions that have led to the development of this article.

References

- Battisti A, Stastny M, Buffo E, Larsson S (2006) A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. *Global Change Biology* 12: 662–671. doi: 10.1111/j.1365-2486.2006.01124.x
- Ben-Tal A, El Ghaoui L, Nemirovski A (2009) Robust Optimization. Princeton Series in Applied Mathematics, Princeton University Press.
- Beven KJ, Pappenberger F, Freer J (2005) Communicating uncertainty as multiple competing hypotheses. American Geophysical Union, Fall Meeting 2005.
- Bogich TL, Liebhold AM, Shea K (2008) To sample or eradicate? A cost minimization model for monitoring and managing an invasive species. *Journal of Applied Ecology* 45: 1134–1142. doi: 10.1111/j.1365-2664.2008.01494.x
- Buckley YM, Anderson S, Catterall CP, Corlett RT, Engel T, Gosper CR, Nathan R, Richardson DM, Setter M, Spiegel O, Vivian-Smith G, Voigt FA, Weir JES, Westcott DA (2006) Management of plant invasions mediated by frugivore interactions. *Journal of Applied Ecology* 43: 848–857. doi: 10.1111/j.1365-2664.2006.01210.x
- Cacho OJ, Spring D, Hester S, Mac Nally R (2010) Allocating surveillance effort in the management of invasive species: A spatially-explicit model. *Environmental Modelling and Software* 25(4): 444–454. doi: 10.1016/j.envsoft.2009.10.014
- Carrasco LR, Baker R, MacLeod A, Knight JD, Mumford JD (2009) Optimal and robust control of invasive alien species spreading across homogeneous landscapes. *Journal of the Royal Society Interface* 7(44): 529–540. doi: 10.1098/rsif.2009.0266
- Carrasco LR, Harwood TD, Toepfer S, MacLeod A, Levay N, Kiss J, Baker RHA, Mumford JD, Knight JD (2010) Dispersal kernels of the invasive alien western corn rootworm and the effectiveness of buffer zones in eradication programmes in Europe. *Annals of Applied Biology* 156: 63–77. doi: 10.1111/j.1744-7348.2009.00363.x
- Chadès I, Martin TG, Nicol S, Burgman MA, Possingham HP, Buckley YM (2011) General rules for managing and surveying networks of pests, diseases, and endangered species. *Proceedings of the National Academy of Sciences* 108: 8323–8328. doi: 10.1073/pnas.1016846108
- Chamberlin TC (1890) The method of multiple working hypotheses. *Science* 15: 92–96.
- Chapman JW, Nesbit RL, Burgin LE, Reynolds DR, Smith AD, Middleton DR, Hill JK (2010) Flight orientation behaviours promote optimal migration trajectories in high-flying insects. *Science* 327(5966): 682–685. doi: 10.1126/science.1182990
- Costello C, McAusland C (2003) Protectionism, trade, and measures of damage from exotic species introductions. *American Journal of Agricultural Economics* 85(4): 964–975. doi: 10.1111/1467-8276.00500
- Coutts SR, van Klinken RD, Yokomizo H, Buckley YM (2011) What are the key drivers of spread in invasive plants: dispersal, demography or landscape: and how can we use this knowledge to aid management? *Biological Invasions* 13: 1649–1661. doi: 10.1007/s10530-010-9922-5
- Demon I, Cunniffe NJ, Marchant BP, Gilligan CA, van den Bosch F (2011) Spatial sampling to detect an invasive pathogen outside of an eradication zone. *Phytopathology* 101: 725–731. doi: 10.1094/PHYTO-05-09-0120

- Deveson ED, Drake VA, Hunter DM, Walker PW, Wang HK (2005) Evidence from traditional and new technologies for northward migrations of Australian plague locusts (*Chortoicetes terminifera*) (Walker) (Orthoptera: Acrididae) to western Australia. *Austral Ecology* 30: 928–943. doi: 10.1111/j.1442-9993.2005.01536.x
- Drake DAR, Mandrak NE (2010) Least-cost transportation networks predict spatial interaction of invasion vectors. *Ecological Applications* 20: 2286–2299. doi: 10.1890/09-2005.1
- Dupin M, Reynaud P, Jarošík V, Baker R, Brunel S, Eyre D, Pergl J, Makowski D (2011) Effects of the training dataset characteristics on the performance of nine species distribution models: Application to *Diabrotica virgifera virgifera*. *PLoS ONE* 6: e20957. doi: 10.1371/journal.pone.0020957
- Elith J, Leathwick JR (2009) Species Distribution Models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697. doi: 10.1146/annurev.ecolsys.110308.120159
- Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution* 1(4): 330–342. doi: 10.1111/j.2041-210X.2010.00036.x
- Epanchin-Niell RS, Haight RG, Berek L, Kean JM, Liebhold AM (2012) Optimal surveillance and eradication of invasive species in heterogeneous landscapes. *Ecology Letters* 15(8): 803–812. doi: 10.1111/j.1461-0248.2012.01800.x
- Facon B, David P (2006) Metapopulation dynamics and biological invasions: A spatially explicit model applied to a freshwater snail. *American Naturalist* 168: 769–783. doi: 10.1086/508669
- FAO (2006) International Standards for Phytosanitary Measures: 1 to 24. Rome, Secretariat of the International Plant Protection Convention.
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38–49. doi: 10.1017/S0376892997000088
- Fletcher CS, Westcott D (2013) Dispersal and the design of effective management strategies for plant invasions: matching scales for success. *Ecological Applications*. doi: 10.1890/12-2059.1
- Florec V, Sadler RJ, White B, Dominiak B (2013) Choosing the battles: The economics of area wide pest management for Queensland fruit fly. *Food Policy* 38: 203–213.
- García Adeva JJ, Botha JH, Reynolds M (2012) A simulation modelling approach to forecast establishment and spread of *Bactrocera* fruit flies. *Ecological Modelling* 227: 93–108. doi: 10.1016/j.ecolmodel.2011.11.026
- Gilbert M, Liebhold A (2010) Comparing methods for measuring the rate of spread of invading populations. *Ecography* 33: 809–817. doi: 10.1111/j.1600-0587.2009.06018.x
- Greene DF, Calogeropoulos C (2002) Measuring and modelling seed dispersal of terrestrial plants. In: Bullock JM, Kenward RE, Hails RS (Eds) *Dispersal Ecology: the 42nd symposium of the British Ecological Society held at the University of Reading, 2–5 April 2001*. Blackwell Science, Oxford.
- Grimm V, Railsback SF (2005) Individual-based Modeling and Ecology. Princeton University Press, i-xvi, 428 pp.

- Guichard S, Kriticos DJ, Leriche A, Kean JM, Worner SP (2012) Individual-based modelling of moth dispersal to improve biosecurity incursion response. *Journal of Applied Ecology* 49: 287–296. doi: 10.1111/j.1365-2664.2011.02072.x
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186. doi: 10.1016/S0304-3800(00)00354-9
- Hansen LP, Sargent TJ (2007) Robustness. Princeton University Press.
- Hanski I (1999) Metapopulation Ecology. Oxford University Press, Oxford.
- Harwood TD, Tomlinson I, Potter CA, Knight JD (2011) Dutch elm disease revisited: past, present and future management in Great Britain. *Plant Pathology* 60: 545–555. doi: 10.1111/j.1365-3059.2010.02391.x
- Harwood TD, Xu X, Pautasso M, Jeger MJ, Shaw MW (2009) Epidemiological risk assessment using linked network and grid based modelling: *Phytophthora ramorum* and *Phytophthora kernoviae* in the UK. *Ecological Modelling* 220(23): 3353–3361. doi: 10.1016/j.ecolmodel.2009.08.014
- Hastings A (1996) Models of spatial spread: A synthesis. *Biological Conservation* 78: 143–148. doi: 10.1016/0006-3207(96)00023-7
- Higgins SI, Richardson DM (1996) A review of models of alien plant spread. *Ecological Modelling* 87: 249–265. doi: 10.1016/0304-3800(95)00022-4
- Higgins SI, Richardson DM (1998) Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. *Plant Ecology* 135: 79–93. doi: 10.1023/A:1009760512895
- Higgins SI, Richardson DM, Cowling RM (1996) Modeling invasive plant spread: The role of plant-environment interactions and model structure. *Ecology* 77: 2043–2054. doi: 10.2307/2265699
- Higgins SI, Richardson DM, Cowling RM (2001) Validation of a spatial simulation model of a spreading alien plant population. *Journal of Applied Ecology* 38: 571–584. doi: 10.1046/j.1365-2664.2001.00616.x
- Higgins SI, Clark JS, Nathan R, Hovestadt T, Schurr F, Fragoso JMV, Aguiar MR, Ribbens E, Lavorel S (2003) Forecasting plant migration rates: managing uncertainty for risk assessment. *Journal of Ecology* 91: 341–347. doi: 10.1046/j.1365-2745.2003.00781.x
- Hilborn R, Mangel M (1997) The ecological detective: confronting models with data. Princeton University Press, Princeton, NJ.
- Hlasny V (2011) The stock of invasive insect species and its economic determinants. *Journal of Economic Entomology* 104 (3): 764–772. doi: 10.1603/EC10422
- Holling CS (1978) Adaptive Environmental Assessment and Management. John Wiley & Sons, London.
- Hooten MB, Wikle CK (2008) A hierarchical Bayesian non-linear spatio-temporal model for the spread of invasive species with application to the Eurasian Collared-Dove. *Environmental and Ecological Statistics* 15: 59–70. doi: 10.1007/s10651-007-0040-1
- Hopkinson RF, Soroka JJ (2010) Air trajectory model applied to an in-depth diagnosis of potential diamondback moth infestations on the Canadian Prairies. *Agricultural and Forest Meteorology* 150: 1–11. doi: 10.1016/j.agrformet.2009.07.015

- Jones CC, Acker SA, Halpern CB (2010) Combining local- and large-scale models to predict the distributions of invasive plant species. *Ecological Applications* 20: 311–326. doi: 10.1890/08-2261.1
- Jongejans E, Skarpaas O, Shea K (2008) Dispersal, demography and spatial population models for conservation and control management. *Perspectives in Plant Ecology, Evolution and Systematics* 9: 153–170. doi: 10.1016/j.ppees.2007.09.005
- Jørgensen SE, Bendoricchio G (2001) Fundamentals of Ecological Modelling. Elsevier, Oxford.
- Kanarek AR, Webb CT, Barfield M, Holt RD (2012) Allee effects, aggregation, and invasion success. *Theoretical Ecology*, online first. doi: 10.1007/s12080-012-0167-z
- Katul GG, Proporato A, Nathan R, Siqueira M, Soons MB, Poggi D, Horn HS, Levin SA (2005) Mechanistic analytical models for long-distance seed dispersal by wind. *The American Naturalist* 166: 368–381. doi: 10.1086/432589
- Kawasaki K, Takasu F, Caswell H, Shigesada N (2006) How does stochasticity in colonization accelerate the speed of invasion in a cellular automaton model? *Ecological Research* 21: 334–345. doi: 10.1007/s11284-006-0166-x
- Kot M, Lewis MA, van den Driessche P (1996) Dispersal data and the spread of invading organisms. *Ecology* 77: 2027–2042. doi: 10.2307/2265698
- Kriticos DJ, Randall RP (2001) A comparison of systems to analyse potential weed distributions. In: Groves RH, Panetta FD, Virtue JG (Eds) *Weed Risk Assessment*. CSIRO Publishing, Melbourne, Australia, 61–79.
- Kriticos D, Sutherst R, Brown J, Adkins S, Maywald G (2003) Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. *Journal of Applied Ecology* 40: 111–124. doi: 10.1046/j.1365-2664.2003.00777.x
- Kriticos DJ, Morin L, Leriche A, Anderson RC, Caley P (2013a) Combining a climatic niche model of an invasive fungus with its host species distribution to identify risks: *Puccinia psidii* sensu lato in Australia. *PLoS ONE* 8: e64479. doi: 10.1371/journal.pone.0064479
- Kriticos DJ, Leriche A, Palmer D, Cook DC, Brockerhoff EG, Stephens AEA, Watt MS (2013b) Linking climate suitability, spread rates and host-impact when estimating the potential costs of invasive pests. *PLoS ONE* 8: e54861. doi: 10.1371/journal.pone.0054861
- Kunz TH, Gauthreaux SA, Hristov NI, Horn JW, Jones G, Kalko EKV, Larkin RP, McCracken GF, Swartz SM, Srygley RB, Dudley R, Westbrook JK, Wikelski M (2008) Aeroecology: probing and modeling the aerosphere. *Integrative and Comparative Biology* 48: 1–11. doi: 10.1093/icb/icn037
- Leighton PA, Koffi JK, Pelcat Y, Lindsay LR, Ogden NH (2012) Predicting the speed of tick invasion: an empirical model of range expansion for the Lyme disease vector *Ixodes scapularis* in Canada. *Journal of Applied Ecology* 49(2): 457–464. doi: 10.1111/j.1365-2664.2012.02112.x
- Leskinen M, Markkula I, Kostinen J, Pylkkö P, Ooperi S, Siljamo P, Ojanen H, Raiskio S, Tiilikka K (2011) Pest insect immigration warning by an atmospheric dispersion model, weather radars and traps. *Journal of Applied Entomology* 135(1–2): 55–67. doi: 10.1111/j.1439-0418.2009.01480.x

- Liebhold AM, Tobin PC (2008) Population ecology of insect invasions and their management. *Annual Review of Entomology* 53: 387–408. doi: 10.1146/annurev.ento.52.110405.091401
- Lindstrom T, Hakansson N, Wennergren U (2011) The shape of the spatial kernel and its implications for biological invasions in patchy environments. *Proceedings of the Royal Society B-Biological Sciences* 278: 1564–1571. doi: 10.1098/rspb.2010.1902
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz F (2000) Biotic Invasions: Causes, epidemiology, global consequences and control. *Ecological Applications* 10(3): 689–710. doi: 10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2
- Marjoram P, Molitor J, Plagnol V, Tavaré S (2003) Markov chain Monte Carlo without likelihoods. *Proceedings of the National Academy of Sciences* 100: 15324–15328. doi: 10.1073/pnas.0306899100
- Mau-Crimmins TM, Schussman HR, Geiger EL (2006) Can the invaded range of a species be predicted sufficiently using only native-range data? Lehmann lovegrass (*Eragrostis lehmanniana*) in the southwestern United States. *Ecological Modelling* 193: 736–746. doi: 10.1016/j.ecolmodel.2005.09.002
- Merow C, LaFleur N, Silander JJA, Wilson AM, Rubega M (2011) Developing dynamic mechanistic species distribution models: Predicting bird-mediated spread of invasive plants across northeastern North America. *The American Naturalist* 178: 30–43. doi: 10.1086/660295
- Monty A, Stainier C, Lebeau F, Pieret N, Mahy G (2008) Seed rain pattern of the invasive weed *Senecio inaequidens* (Asteraceae). *Belgian Journal of Botany* 141: 51–63.
- Moslonka-Lefebvre M, Finley A, Dorigatti I, Dehnen-Schmutz K, Harwood T, Jeger MJ, Xu XM, Holdenrieder O, Pautasso M (2011) Networks in plant epidemiology: From genes to landscapes, countries, and continents. *Phytopathology* 101: 392–403. doi: 10.1094/PHYTO-07-10-0192
- Murphy HT, Hardesty BD, Fletcher CS, Metcalfe DJ, Westcott DA, Brooks SJ (2008) Predicting dispersal and recruitment of *Miconia calvescens* (Melastomataceae) in Australian tropical rainforests.
- Nathan R, Katul GG, Bohrer G, Kuparinen A, Soons MB, Thompson SE, Trakhtenbrot A, Horn HS (2011) Mechanistic models of seed dispersal by wind. *Theoretical Ecology* 4: 113–132. doi: 10.1007/s12080-011-0115-3
- Nathan R, Sapir N, Trakhtenbrot A, Katul GG, Bohrer G, Otte M, Avissar R, Soons MB, Horn HS, Wikelski M, Levin SA (2005) Long-distance biological transport processes through the air: can nature's complexity be unfolded in silico. *Diversity and Distributions* 11: 131–137. doi: 10.1111/j.1366-9516.2005.00146.x
- Nehrbass N, Winkler E (2007) Is the Giant Hogweed still a threat? An individual-based modeling approach for local invasion dynamics of *Heracleum mantegazzianum*. *Ecological Modelling* 201: 377–384. doi: 10.1016/j.ecolmodel.2006.10.004
- Nehrbass N, Winkler E, Mullerova J, Pergl J, Pysek P, Perglova I (2007) A simulation model of plant invasion: long-distance dispersal determines the pattern of spread. *Biological Invasions* 9: 383–395. doi: 10.1016/j.ecolmodel.2006.10.004

- Nenzén HK, Swab RM, Keith DA, Araújo MB (2012) demoniche – an R-package for simulating spatially-explicit population dynamics. *Ecography* 35: 577–580. doi: 10.1111/j.1600-0587.2012.07378.x
- Neubert MG, Caswell H (2000) Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* 81: 1613–1628. doi: 10.1890/0012-9658(2000)081[1613:DADCAS]2.0.CO;2
- NOAA (2011) The NCEP/NCAR Reanalysis Project at the NOAA/ESRL Physical Sciences Division. <http://www.esrl.noaa.gov/psd/data/reanalysis/reanalysis.shtml>
- Overcamp TJ (1976) A general Gaussian diffusion-deposition model for elevated point sources. *Journal of Applied Meteorology* 15: 1167–1171. doi: 10.1175/1520-0450(1976)015<1167:AGGDDM>2.0.CO;2
- Paini DR, Yemshanov D (2012) Modelling the arrival of invasive organisms via the international marine shipping network: a Khapra beetle study. *PLoS ONE* 7: e44589. doi: 10.1371/journal.pone.0044589
- Parker IM (2000) Invasion dynamics of *Cytisus scoparius*: A matrix model approach. *Ecological Applications* 10: 726–743. doi: 10.1890/1051-0761(2000)010[0726:IDOCSA]2.0.CO;2
- Parry HR, Aurambout J-P, Kriticos DJ (2011) Having your cake and eating it: A modelling framework to combine process-based population dynamics and dispersal simulation. In: Chan F, Marinova D, Anderssen RS (Eds) MODSIM2011, 19th International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, December 2011. <http://www.mssanz.org.au/modsim2011/E16/parry.pdf>
- Perrings C, Williamson M, Dalmazzone S (2000) The Economics of Biological Invasions. Edward Elgar Publishing Ltd., Cheltenham, UK.
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259. doi: 10.1016/j.ecolmodel.2005.03.026
- Pimentel D (2011) Biological Invasions: Economic and Environmental Costs of Alien Plant, Animal, and Microbe Species (Second edition). CRC Press, Boca Raton, FL, USA. doi: 10.1201/b10938
- Pitt JPW, Kriticos DJ, Dodd MB (2011) Temporal limits to simulating the future spread pattern of invasive species: *Buddleja davidii* in Europe and New Zealand. *Ecological Modelling* 222: 1880–1887. doi: 10.1016/j.ecolmodel.2011.03.023
- 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. doi: 10.1890/08-1777.1
- Renton M, Savage D, Chopard J (2011) A general spatially-explicit model to inform rapid response to new biological invasions: why do we need one and what should it look like? In: Chan F, Marinova D, Anderssen RS (Eds) MODSIM2011, 19th International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, December 2011. <http://www.mssanz.org.au/modsim2011/E16/renton.pdf>
- Restif O, Hayman DTS, Pulliam JRC, Plowright RK, George DB, Luis AD, Cunningham AA, Bowen RA, Fooks AR, O'Shea TJ, Wood JLN, Webb CT (2012) Model-guided fieldwork:

- practical guidelines for multidisciplinary research on wildlife ecological and epidemiological dynamics. *Ecology Letters* 15: 1083–1094. doi: 10.1111/j.1461-0248.2012.01836.x
- Robinet C, Roques A, Pan H, Fang G, Ye J, Zhang Y, Sun J (2009) Role of human-mediated dispersal in the spread of the pinewood nematode in China. *PLoS ONE* 4(2): e4646. doi: 10.1371/journal.pone.0004646
- Robinet C, Kehlenbeck H, Kriticos DJ, Baker RHA, Battisti A, Brunel S, Dupin M, Eyre D, Faccoli M, Ilieva Z, Kenis M, Knight J, Reynaud P, Yart A, van der Werf W (2012) A suite of models to support the quantitative assessment of spread in pest risk analysis. *PLoS ONE* 7: e43366. doi: 10.1371/journal.pone.0043366
- Rochester WA, Dillon ML, Fitt GP, Zalucki MP (1996) A simulation model of the long-distance migration of *Helicoverpa* spp. moths. *Ecological Modelling* 86: 151–156. doi: 10.1016/0304-3800(95)00043-7
- Royama T (1992) Analytical Population Dynamics. Chapman & Hall, London, UK. doi: 10.1007/978-94-011-2916-9
- Royle JA, Kéry M, Gautier R, Schmid H (2007) Hierarchical spatial models of abundance and occurrence from imperfect survey data. *Ecological Monographs* 77: 465–481. doi: 10.1890/06-0912.1
- Rutherford ES, Rose KA, Mills EL, Forney JL, Mayer CM, Rudstam LG (1999) Individual-based model simulations of a zebra mussel (*Dreissena polymorpha*) induced energy shunt on walleye (*Stizostedion vitreum*) and yellow perch (*Perca flavescens*) populations in Oneida Lake, New York. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 2148–2160. doi: 10.1139/f99-133
- Saltelli A, Ratto M, Andres T, Campolongo F, Cariboni J, Gatelli D, Saisana M, Tarantola S, Young P (2008) Chapter 5 Factor Mapping and Meta-modelling. In: Saltelli et al. Global Sensitivity Analysis: The Primer. John Wiley & Sons, Chichester.
- Savage D, Chopard J, Renton M (in press) Requirements, design and implementation of a general model of biological invasion. *Ecological Modelling*.
- Savage D, Barbetti MJ, MacLeod WJ, Salam MU, Renton M (2011) Can mechanistically parameterised, anisotropic dispersal kernels provide a reliable estimate of wind-assisted dispersal? *Ecological Modelling* 222: 1673–1682. doi: 10.1016/j.ecolmodel.2011.03.003
- Scott RW, Achtemeier GL (1987) Estimating pathways of migrating insects carried in atmospheric winds. *Environmental Entomology* 16: 1244–1254.
- See KE, Feist BE (2010) Reconstructing the range expansion and subsequent invasion of introduced European green crab along the west coast of the United States. *Biological Invasions* 12: 1305–1318. doi: 10.1007/s10530-009-9548-7
- Shamoun-Baranes J, Bouten W, Emiel van Loon E (2010) Integrating meteorology into research on migration. *Integrative and Comparative Biology* 50(3): 280–292. doi: 10.1093/icb/icq011
- Sharov AA, Liebhold AM (1998) Model of slowing the spread of gypsy moth (*Lepidoptera: Lymantriidae*) with a barrier zone. *Ecological Applications* 8: 1170–1179. doi: 10.1890/1051-0761(1998)008[1170:MOSTSO]2.0.CO;2
- Shigesada N, Kawasaki K (1997) Biological invasions: Theory and Practice. In: May RM, Harvey PH (Eds) Oxford University Press, Oxford, 205 pp.

- Shigesada N, Kawasaki K, Takeda Y (1995) Modeling stratified diffusion in biological invasions. *American Naturalist* 146: 229–251.
- Simberloff D, Parker IM, Windle PN (2005) Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment* 3(1): 12–20. doi: 10.1890/1540-9295(2005)003[0012:ISPMAF]2.0.CO;2
- Simberloff D (2013) Invasive Species: What everyone needs to know. Oxford University Press, Oxford, 224 pp.
- Skellam JG (1951) Random dispersal in theoretical populations. *Biometrika* 38: 196–218.
- Skelsey P, Rossing WAH, Kessel GJT, van der Werf W (2010) Invasion of *Phytophthora infestans* at the landscape level: How do spatial scale and weather modulate the consequences of spatial heterogeneity in host resistance? *Phytopathology* 100: 1146–1161. doi: 10.1094/PHYTO-06-09-0148
- Sniedovich M (2010) A bird's view of info-gap decision theory. *Journal of Risk Finance* 11(3): 268–283. doi: 10.1108/15265941011043648
- Sutherst RW, Bourne AS (2009) Modelling non-equilibrium distributions of invasive species: a tale of two modelling paradigms. *Biological Invasions* 11: 1231–1237. doi: 10.1007/s10530-008-9335-x
- Travis JMJ, Dytham C (2002) Dispersal evolution during invasions. *Evolutionary Ecology Research* 4: 1119–1129.
- Turchin P (1998) Quantitative Analysis of Movement. Sinauer, Sunderland, MA.
- van Dorp D, Schippers P, van Groenendael JM (1997) Migration rates of grassland plants along corridors in fragmented landscapes assessed with a cellular automation model. *Landscape Ecology* 12: 39–50. doi: 10.1007/BF02698206
- von Neumann J (1951) The general and logical theory of automata. In: Jeffress LA (Ed) *Cerebral Mechanisms in Behavior – The Hixon Symposium*. John Wiley & Sons, New York, 1–31.
- Waage JK, Fraser RW, Mumford JD, Cook DC, Wilby A (2005) A New Agenda for Biosecurity. Department for Food, Environment and Rural Affairs, London, 198 pp.
- Webber BL, Yates CJ, Le Maitre DC, Scott JK, Kriticos DJ, Ota N, McNeill A, Le Roux JJ, Midgley GF (2011) Modelling horses for novel climate courses: insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models. *Diversity and Distributions* 17: 978–1000. doi: 10.1111/j.1472-4642.2011.00811.x
- Wiegand T, Moloney KA (2004) Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 104: 209–229. doi: 10.1111/j.0030-1299.2004.12497.x
- Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology & Evolution* 24: 136–144. doi: 10.1016/j.tree.2008.10.007
- With KA (2002) The landscape ecology of invasive spread. *Conservation Biology* 16: 1192–1203. doi: 10.1046/j.1523-1739.2002.01064.x
- Wolfram S (1983) Statistical mechanics of cellular automata. *Reviews of Modern Physics* 55: 601–644. doi: 10.1103/RevModPhys.55.601

Yakov B-H (2006) Info-Gap Theory: Decisions Under Severe Uncertainty, 2nd edition. Academic Press, London.

Yonow T, Sutherst RW (1998) The geographical distribution of the Queensland fruit fly, *Bactrocera (Dacus) tryoni*, in relation to climate. Australian Journal of Agricultural Research 49: 935–953. doi: 10.1071/A97152

An assessment of the benefits of yellow Sigatoka (*Mycosphaerella musicola*) control in the Queensland Northern Banana Pest Quarantine Area

David C. Cook^{1,2,3,4}, Shuang Liu^{2,4,5}, Jacqueline Edwards^{2,6}, Oscar N. Villalta^{2,6}, Jean-Philippe Aurambout^{2,7}, Darren J. Kriticos^{2,5,8,9}, Andre Drenth¹⁰, Paul J. De Barro^{2,11}

1 Department of Agriculture and Food, Bunbury, Western Australia, Australia **2** Plant Biosecurity Cooperative Research Centre, Bruce, Australian Capital Territory, Australia **3** The University of Western Australia, Crawley, Western Australia, Australia **4** Australian Centre for Biosecurity and Environmental Economics, Canberra, Australian Capital Territory, Australia **5** CSIRO Ecosystem Sciences, Canberra, Australian Capital Territory, Australia **6** Department of Primary Industries, Knoxfield, Victoria, Australia **7** Department of Primary Industries, Parkville, Victoria, Australia **8** Charles Sturt University, Barton, Australian Capital Territory, Australia **9** The University of Minnesota, Minneapolis, Minnesota, United States **10** The University of Queensland, Dutton Park, Queensland, Australia **11** CSIRO Ecosystem Sciences, Dutton Park, Queensland, Australia

Corresponding author: David C. Cook (david.cook@agrif.wa.gov.au)

Academic editor: I. Kühn | Received 16 August 2012 | Accepted 29 April 2013 | Published 13 September 2013

Citation: Cook DC, Liu S, Edwards J, Villalta ON, Aurambout J-P, Kriticos DJ, Drenth A, De Barro PJ (2013) An assessment of the benefits of yellow Sigatoka (*Mycosphaerella musicola*) control in the Queensland Northern Banana Pest Quarantine Area. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 67–81. doi: 10.3897/neobiota.18.3863

Abstract

The banana leaf spotting disease yellow Sigatoka is established and actively controlled in Australia through intensive chemical treatments and diseased leaf removal. In the State of Queensland, the State government imposes standards for de-leaving to minimise the risk of the disease spreading in 6 banana pest quarantine areas. Of these, the Northern Banana Pest Quarantine Area is the most significant in terms of banana production. Previous regulations imposed obligations on owners of banana plants within this area to remove leaves from plants with visible spotting on more than 15 per cent of any leaf during the wet season. Recently, this leaf disease threshold has been lowered to 5 per cent. In this paper we examine the likely impact this more-costly regulation will have on the spread of the disease. We estimate that the average net benefit of reducing the diseased leaf threshold is only likely to be \$1.4 million per year over the next 30 years, expressed as the annualised present value of tightened regulation. This result varies substantially when the timeframe of the analysis is changed, with shorter time frames indicating poorer net returns from the change in protocols. Overall, the benefit of the regulation change is likely to be minor.

Keywords

Biosecurity, invasive alien species, banana pathogen, yellow Sigatoka

Introduction

The Sigatoka disease complex affects banana cultivation in many countries. The disease yellow Sigatoka (*Mycosphaerella musicola*) is established and actively controlled in Australia through intensive fungicide treatments and diseased leaf removal (Henderson et al. 2006). Although less virulent than the malign black Sigatoka (*M. fijiensis*), *M. musicola* also imposes substantial costs on affected banana growers. This is particularly true for Australia's premier banana growing regions located in the State of Queensland, including the Innisfail-Tully area. In 2011, the State as a whole produced 279.1 thousand tonnes of bananas valued at \$448.3 million from a plantation area of approximately 10 100 hectares (ABS 2012).

In all areas of the State where *M. musicola* occurs, grower costs are incurred through compliance with government-imposed standards for de-leaving to minimise the risk of the disease's spread. The Plant Protection Regulation 2002 was put in place under the Plant Protection Act 1989 which defined 6 banana pest quarantine areas (State of Queensland 2002). Of these, the Northern Banana Pest Quarantine Area (NBPQA) is the most significant, encompassing over 80 per cent of the State's banana production. The Plant Protection Regulation 2002 imposed an obligation on the owner of land in a pest quarantine area to treat every banana plant by removing every leaf from the plant that has visible symptoms of *M. musicola* (and another endemic disease, banana leaf speckle (*M. musae*)) on more than 15 per cent of any leaf at any time between 1 November and 31 May or on more than 30 per cent of any leaf at any time between 1 June and 31 October.

An amendment to the Plant Protection Regulation 2002, the Plant Protection Amendment Regulation (No. 4) 2003, was subsequently put in place in response to concerns that the de-leaving standards initially imposed were too permissive. In particular, during wet season conditions in the NBPQA the 15 per cent de-leaving threshold was deemed insufficient to prevent *M. musicola* and *M. musae* from spreading. Moreover, the 30 per cent action level in the dry season was thought to be far too high for wet weather conditions highly conducive to disease spread (State of Queensland 2003). The Amendment imposed a lower threshold of 5 per cent throughout the year in the NBPQA.

As deleterious as these amended regulations appear to be in terms of the foliage carried by commercial banana plants, the impact on production volume is likely to be minimal. During their life, individual banana plants may produce 30 or more leaves, which is surplus to their photosynthetic needs. The oldest leaves are shed at a rate of approximately 1 leaf every 10 to 12 days so that when the fruit bunch emerges from the top of the pseudostem the plant has an average of 15 leaves. After the bunch shoots no

new leaves are produced. The oldest leaves of the plant continue to fall until, at harvest, between 6 and 8 leaves remain (Ostmark 1974).

While the incidence of leaf disease is likely to be reduced if stricter thresholds are implemented and maintained over time, additional costs to banana growers in the NBPQA will apply. These include substantial increases in chemical treatment and application costs in addition to more rigorous de-leaving cycles. In this paper we estimate the likely change in net returns to the banana industry in the NBPQA from adopting the new 5 per cent de-leaving threshold.

Methods

The stochastic simulation model used in this assessment determines total *expected* (or probability-weighted) damage from *M. musicola* in the NBPQA over a 30-year period under both a 15 per cent and a 5 per cent de-leaving threshold. Uncertain or variable parameters are specified as probability distributions. 10 000 model iterations are run using values randomly sampled across the range of each distribution using a Latin hypercube sampling algorithm.

The total damage banana producers in the NAPQA experience because of the disease in time period t (d_t) is estimated by:

$$d_t = Y_t P_t A_t + V_t A_t \quad (1)$$

where: Y_t is the mean change in banana yield resulting from infection (assumed 100 per cent) in year t ; P_t is the prevailing domestic price for bananas in year t ; V_t is the increase in variable cost of production per hectare induced by *M. musicola* on-plantation management methods in year t ; and A_t is the area infected with *M. musicola* in year t .

A stratified diffusion model combining both short and long distance dispersal processes is used to predict A_t . Parameter estimates for this model appear in Table 1, and are explained below.

Note that due to the uncertainty surrounding some of these parameters, they are specified using a range of distributional forms, rather than simple point estimates. Types of distributions used in the table include: (a) pert – a type of beta distribution specified using minimum, most likely (or skewness) and maximum values often preferred when parameters are reliant a number of sources (or expert opinions) since the mean is relatively insensitive to minimum and maximum values compared to the most likely value; (b) uniform – a rectangular distribution bounded by minimum and maximum values used to highlight the fact that there is little known about a parameter (Vose 2008).

The dispersal model is derived from the reaction diffusion models originally developed by Fisher (1937) which have been shown to provide a reasonable approximation of the spread of a diverse range of organisms (Cook et al. 2011a; Dwyer 1992;

Table I. Parameter values

Description	15% de-leaving threshold	5% de-leaving threshold
Detection probability (%).	100	100
Infection diffusion coefficient, D (m^2/yr). [†]	Pert($2.0 \times 10^3, 3.5 \times 10^3, 5.0 \times 10^3$)	Pert($0.0, 1.0 \times 10^2, 2.0 \times 10^2$)
Percentage of total NBPQA plantation area infected in the first time step (%). [‡]	Pert(0.0, 1.5, 3.0)	Pert(0.2, 4)
Minimum area infected, A^{\min} (m^2).	1.0×10^3	1.0×10^3
Maximum area infected, A^{\max} (m^2). [§]	9.8×10^7	9.8×10^7
Intrinsic rate of infection and density increase, $r(\text{yr}^{-1})$. [†]	Pert (0.00, 0.01, 0.02)	Pert (0.00, 0.01, 0.02)
Minimum infection density, N^{\min} (#/ m^2).	1.0×10^{-4}	1.0×10^{-4}
Maximum infection density, K (#/ m^2). [†]	Pert(100, 550, 1000)	Pert(100, 550, 1000)
Minimum number of satellite sites generated in a single time step, S^{\min} (#).	1	1
Maximum number of satellite sites generated in a single time step, S^{\max} (#). [†]	Pert(0, 5, 10)	Pert(0, 5, 10)
Intrinsic rate of new foci generation per unit area of infection, μ (#/ m^2). [†]	Pert($1.0 \times 10^{-2}, 3.0 \times 10^{-2}, 5.0 \times 10^{-2}$)	Pert($1.0 \times 10^{-2}, 3.0 \times 10^{-2}, 5.0 \times 10^{-2}$)
Demand elasticity. [¶]	Uniform(-1.1, -1.0)	Uniform(-1.1, -1.0)
Prevailing market price of bananas in the first time step (\$/T). [§]	1 900	1 900
Maximum area considered for eradication, A^{erad} (ha).	0	0
Treatment costs upon detection – chemical (\$/ha). [¶]	Pert($8.0 \times 10^3, 1.1 \times 10^4, 1.3 \times 10^4$)	Pert($1.6 \times 10^4, 5.0 \times 10^4, 6.6 \times 10^4$)
Treatment costs upon detection – de-leaving (\$/ha). [#]	Pert($1.4 \times 10^3, 2.1 \times 10^3, 2.8 \times 10^3$)	Pert($2.1 \times 10^3, 3.1 \times 10^3, 3.2 \times 10^3$)
Yield reduction despite control (%).	Pert(0.0, 2.5, 5.0)	Pert(0.0, 0.5, 1.0)
Discount rate (%). ^{††}	5	5

[†] Specified with reference to Cook (2003) and Waage et al. (2005).

[‡] Derived from Peterson et al. (2005).

[§] ABS (2012), Note 1ha = 10 000m².

[¶] Ulubasoglu et al. (2011).

[#] Assumes: (i) average density of planting of 2 000 stems/ha and removal, (ii) control of *M. musicola* in the NBPQA involves applications of dithane (at 3kg/ha or \$21.60/ha) and oil (at 3L/ha or \$8.85/ha) at weekly intervals during the wet season (Cook 2003); (iii) it is desirable for growers to rotate the use of dithane and oil with propiconazole (at 0.3L/ha or \$22.20/ha) to manage resistance (Cook 2003); (iv) 15 to 25 cycles of fungicides are used for control of *M. musicola* in the NBPQA to comply with a 15% de-leaving threshold; (v) an additional 5 to 10 spray cycles are needed to comply with a 5% de-leaving threshold.

^{††} De-leaving plantations to control *M. musicola* to a 15% threshold occurs up to 15 times per season. Assume an additional 5 to 10 de-leaving cycles are necessary to achieve a 5% threshold at a cost of \$140/ha each.

^{††} Commonwealth of Australia (2006).

Holmes 1993; McCann et al. 2000; Okubo and Levin 2002). These models assert that an invasion diffusing from a point source will eventually reach a constant asymptotic radial spread rate of $2\sqrt{rD_j}$ in all directions, where r describes a growth factor for *M.*

musicola per year in the NBPQA (assumed constant over all infected sites) and D_j is a diffusion coefficient for an infected site with an age index j (indicating the time step in which the site was originally formed) in the NBPQA (Cook et al. 2011a; Hengeveld 1989; Lewis 1997; Shigesada and Kawasaki 1997). Hence, we assume that an original infection in a previously unaffected area takes place in a homogenous environment within the NBPQA and expands by a diffusive process such that area infected at time t , a_{jt} , can be predicted by:

$$a_{jt} = \pi(2t\sqrt{rD_j})^2 = 4D_j\pi r t^2. \quad (2)$$

We assume D_j is constant across all sites with an age index j , so ignore demographic stochasticity and consequent non-uniform invasion. Since the two control strategies we are considering (i.e. 5 per cent and 15 per cent de-leaving regulations) are very similar, many of the parameters remain the same for both scenarios. But, D is assumed to be lower under the 5 per cent de-leaving threshold due to increased chemical suppression limiting local dispersal opportunities for the disease.

The density of *M. musicola* infection within a_{jt} influences the control measures required to counter the effects of infection and thus partially determines the value of A_t . We assume that within each site with age index j affected, the infection density, N_{jt} , grows over time period t following a logistic growth curve until the carrying capacity of the host environment, K_j is reached:

$$N_{jt} = \frac{K_j N_j^{\min} e^{rt}}{K_j + N_j^{\min} (e^{rt} - 1)}. \quad (3)$$

Here, N_j^{\min} is the size of the original infection at site with age index j and r is the intrinsic rate of density increase (assumed to be the same as the intrinsic rate of infection increase) (Cook et al. 2011b). Note that for simplicity we assume N_{jt} and Y_t are independent of one another. In addition to a_{jt} and N_{jt} , the size of A_t depends on the number of nascent foci or *satellite* infection sites in year t , s_t , which can take on a maximum value of s_{\max} in any year (Moody and Mack 1988). These sites result from events external to the initial outbreak itself, such as weather phenomena, animal or human behaviour, which periodically jump the expanding infection beyond the infection front (Cook et al. 2011b). We use a logistic equation to generate changes in s_t as an infectious outbreak continues:

$$s_t = \frac{s^{\max} s^{\min} e^{\mu t}}{s^{\max} + s^{\min} (e^{\mu t} - 1)} \quad (4)$$

where μ is the intrinsic rate of new foci generation (assumed constant over time) and s_{\min} is the minimum number of satellite sites generated.

Given equations (1)-(4), we can express A_t as:

$$A_t = s_t \sum_{j=1}^m (a_{jt} N_{jt}) \text{ where } 0 \leq A_t \leq A^{\max}. \quad (5)$$

Spread area, infection density and the number of foci are combined with the probability of entry and establishment in an expression of probability-weighted, or expected damage over time. Assuming a discount rate δ , the present value of expected damage after t time periods (TC^P) is:

$$TC^P = \sum_{t=1}^{\tau} (1 - \delta)^{-t} \cdot d_t. \quad (6)$$

This expression provides us with an estimate of infection-induced producer losses over time. It therefore provides an indication of the economic significance of *M. musicola* over time given a de-leafing protocol. If we denote the total expected damage under a 15 per cent and a 5 per cent de-leafing protocol $TC^P_{15\%}$ and $TC^P_{5\%}$, respectively, we can determine the likely change in expected damage (ΔTC^P) from adopting the new 5 per cent protocol as:

$$\Delta TC^P = \Delta TC^P_{15\%} - \Delta TC^P_{5\%}. \quad (7)$$

If indeed the 5 per cent de-leafing protocol is more effective than the previous 15 per cent protocol at reducing *M. musicola* prevalence and impact over time, we would expect $\Delta TC^P > 0$.

Results

M. musicola is assumed to be present within the NBPQA at the beginning of time period 1. Therefore, the resultant expected spread area values calculated from 10 000 iterations of the model are positive, as revealed by Figure 1. Spread is predicted to be very slow in both the 5 per cent and 15 per cent de-leafing protocol scenarios due to the effectiveness of chemical and de-leafing treatments applied simultaneously. The box-whisker plot used in this Figure (and in Figures 2 to 4 to follow) shows the extent of uncertainty in the model predictions dictated by the uncertainty in parameter specification. The box-whisker plot shows the 25th percentile of the frequency distribution of model outcomes, the median (i.e. the 50th percentile), the 75th percentile and remaining values up to and including the 5th and 95th percentiles of the frequency distribution of model outcomes.

Figure 2 illustrates how the resultant $TC^P_{15\%}$ and $TC^P_{5\%}$ (i.e. see equation (6)) are expected to change over the 30-year period of the simulation. Here, the mean values of $TC^P_{15\%}$ and $TC^P_{5\%}$ predicted by the model in each year are plotted with 10th and 50th percentiles of the frequency distribution of model outcomes. All projected costs are discounted at 5 per cent per annum. By the 30th year, $TC^P_{15\%}$ is expected to average just under \$30 million per year, and $TC^P_{5\%}$ just under \$15 million per year.

Note that despite the area affected by the disease remaining relatively constant in both control scenarios, the erosive effects of the discount rate lead to a gradual decline in present value of future expected annual industry damage.

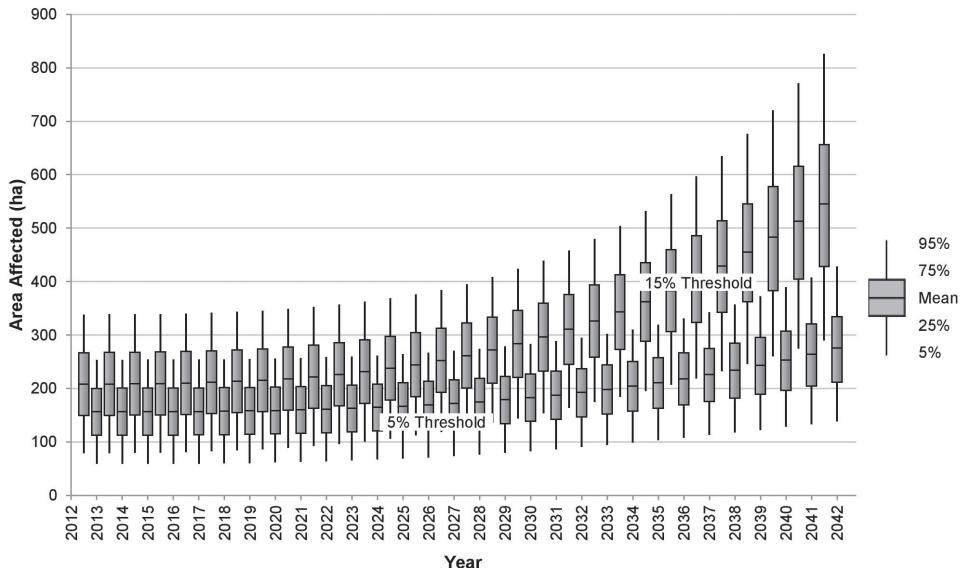


Figure 1. Expected area of commercial banana plantations affected by yellow Sigatoka in Australia under different management guidelines.

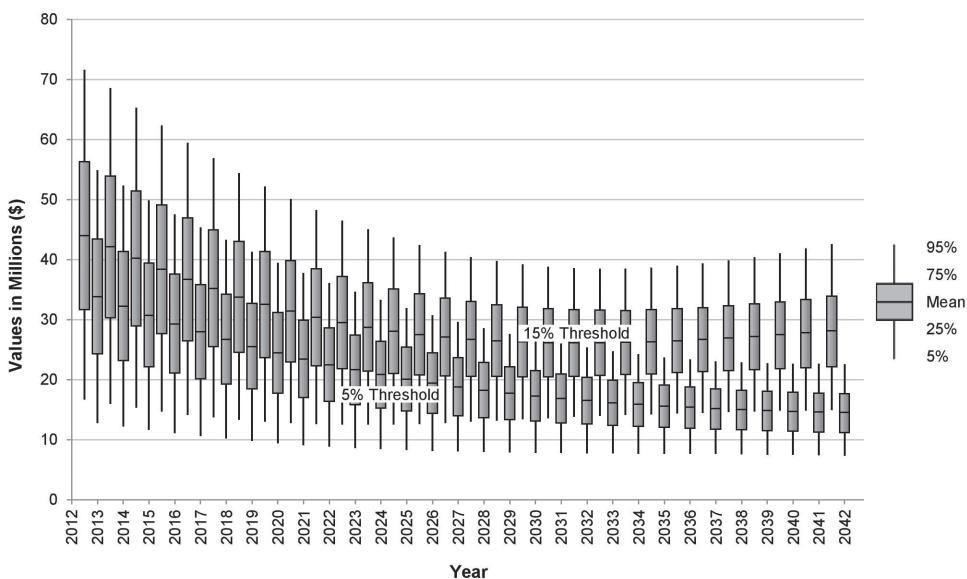


Figure 2. Predicted industry losses from yellow Sigatoka in Australia under different management guidelines.

Figure 3 illustrates how the difference between $TC^P_{15\%}$ and $TC^P_{5\%}$ (i.e. ΔTC^P in equation (7)) is expected to change over time, and therefore the relative merit in the banana industry choosing a 5 per cent de-leaving protocol over a 15 per cent protocol

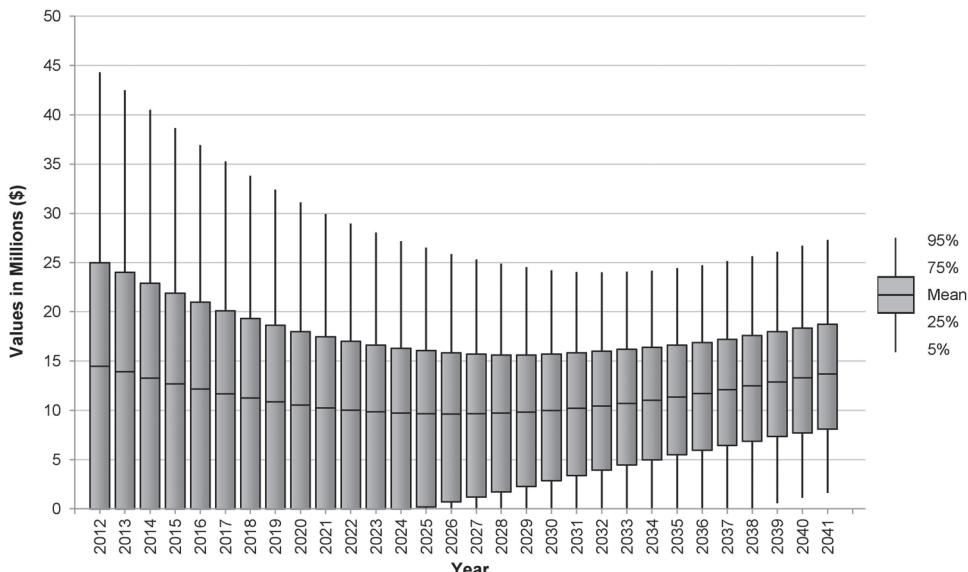


Figure 3. Predicted gross benefit of adopting a 5 per cent de-leaving threshold for yellow Sigatoka suppression in the NBPQA relative to a 15 per cent protocol.

in the NBPQA. Over the 30 years simulated by the mode, the annualised present value of benefit to producers is \$11.3 million. But, as Figure 3 shows there is a large amount of uncertainty associated with predicting this far into the future (i.e. the standard deviation of the benefit estimate is \$9.3 million).

Discussion

Economic research in the area of invasive species has grown substantially in the last 20 years from a modest base (Born et al. 2005; Colautti et al. 2006). Most research has involved retrospective assessments of invasive species impacts and management (Born et al. 2005; Naylor 2000). Where predictive models have been used, analyses have tended to be deterministic, thereby neglecting uncertainties in species behaviour and environmental interactions. For example, State of Queensland (2003) includes a cost benefit analysis of the change in disease threshold in the NBPQA which reveals little about the flow of producer benefits over time. Point estimates of the net producer impact of a 5 per cent de-leaving threshold (-\$50 000 in the first year, -\$20 000 in the second year, \$0 in the third year and \$400 000 by the end of the fourth year) are provided (State of Queensland 2003), but no indication is given about possible variation around these estimates. Moreover, information about their derivation in the Amendment text is not provided.

In contrast, the predictive model presented in this paper provides a more open and transparent means of summarising complex interactions between natural processes and

land managers over time for a policy audience. Policy-makers face a difficult challenge because invasive species impacts change with respect to time, space and other variables in ways that are difficult to predict (Regan et al. 2002). They therefore require tools that are explicit about uncertainty and management options that are both precautionary and adaptive (Doak et al. 2008; Simberloff 2005). Rather than over-simplified point estimates, the model we have developed takes into account system dynamics and conveys the natural variation of the system to decision-makers when analysing the intertemporal effects of changing de-leaving protocols.

Several studies have integrated established ecological models (including reaction-diffusion, stratified diffusion and predator-prey models) with economic management frameworks for invasive species using comparable approaches (Barbier 2001; Cacho et al. 2008; Carrasco et al. 2010; Hyder et al. 2008; Sharov and Liebhold 1998). Others have emphasised spatially explicit approaches using stochastic simulations combining environmental variables and dissemination behaviours to characterise uncertainty in spread patterns over time (Rafoss 2003; Yemshanov et al. 2009). Other recent analytical spatial studies of invasive species spread and control have relied on metapopulation models (Albers et al. 2010; Sanchirico et al. 2010).

At the cost of not producing spatially explicit outputs, our model provides a more accurate estimation of the economic impacts of invasive species by incorporating partial equilibrium models. This approach allows a detailed examination of changes in producer (and consumer) welfare in domestic (e.g. Cook 2008; Heikkila and Peltola 2004; Paarlberg et al. 2003) and export markets (e.g. Acquaye et al. 2005; Cook and Fraser 2008) induced by invasive species. Flow-on effects of incursions to other areas of the economy can also be estimated using general equilibrium models (Wittwer et al. 2005). However, these assume perfect coordination of trading mechanisms and maximise a common sector utility function making it difficult to integrate them with ecological processes (Carrasco et al. 2012).

Similar problems arise with partial equilibrium models due to their aggregated and compact nature, and their integration with ecological spread requires the use of exogenous assumptions regarding the effect that an invasive species will have on the supply curve of the host commodity (Acquaye et al. 2005; Paarlberg et al. 2003). In this analysis we have been explicit about these assumptions with the notes accompanying Table 1 providing technical details of the way we assume grower behaviour is likely to change with a 5 per cent disease threshold compared to a 15 per cent threshold. Specifically, we assume:

- (i) An average density of planting of 2 000 stems per hectare and removal;
- (ii) Control of *M. musicola* in the NBPQA involves applications of dithane (at 3 kg per hectare or \$22 per hectare) and oil (at 3 L per hectare or approximately \$9 per hectare) at weekly intervals during the wet season (Cook 2003);
- (iii) Growers rotate the use of dithane and oil with propiconazole (at 0.3 L per hectare or \$22 per hectare) to manage resistance (Cook 2003);

- (iv) 15 to 25 cycles of fungicides are used for control of *M. musicola* in the NBPQA to comply with a 15 per cent de-leaving threshold, and an additional 5 to 10 spray cycles are needed to comply with a 5 per cent de-leaving threshold;
- (v) De-leaving plantations to control *M. musicola* to a 15 per cent threshold occurs up to 15 times per season, and an additional 5 to 10 de-leaving periods are necessary to achieve a 5 per cent threshold at a cost of \$140 per hectare each.

Extrapolating across the entire NBPQA, these assumptions imply that producer costs will rise by approximately \$43.8 million under the 5 per cent de-leaving threshold (Table 2). This includes both de-leaving and chemical application costs required in areas affected by *M. musicola*. Since the market is closed to imports, the domestic price of bananas will increase as producers pass these cost increases on to consumers. The extent of the price change is predicted in the model using the elasticity of demand (i.e. the ratio of percentage quantity changes over percentage price changes). Thus, our producer behavioural assumptions combine with the spread model to simulate changes in the market over time.

Note that the costs indicated in Table 2 are annualised average costs estimated across the whole NBPQA attributable to compliance with the leaf disease thresholds. The right hand column labelled B-A represents the annualised increase in chemical and de-leaving costs imposed by the lower threshold of 5 per cent. By comparing the present value (i.e. the discounted or real) value of these annual cost increments to the predicted benefits derived from Figure 3, we can estimate the likely change in net returns (i.e. benefits minus costs) to the NBPQA from adopting this lower standard.

While Table 2 summarises our analysis, it does not show the extent to which likely net benefits change depending on the time frame of the analysis. Net returns on a year-by-year basis are shown in Figure 4, which reveals the full extent of uncertainty surrounding possible net returns to the region in each time step. Initially, due to the increased cost of compliance to the 5 per cent leaf disease threshold, net costs (i.e. a surplus of costs over benefits) are likely to result in the short term. However, after a period of time (between 7 and 14 years) the benefits generated by lower *M. musicola* prevalence and impact begin to outweigh compliance costs. By the end of the simulation period, net benefits are likely to be over \$13 million per annum.

On average, over the 30-year model simulation period, the annualised present value of net benefit to the banana industry in the NBPQA from the adoption of the more stringent leaf disease threshold is estimated to be \$1.4 million. Considering this benefit accrues over an area of approximately 10 100 hectares, the impact of the change in disease thresholds appears to be marginal. If we calculate average net returns over a 20-year period, we find that a net cost of the order of -\$3.4 million per annum is likely to result. As Figure 4 clearly shows, this is due to the large net costs concentrated in the early years of adopting the new threshold. The further forward in time we project, the larger the likely returns to the banana industry of imposing the stricter leaf disease threshold.

Given the intertemporal nature of cost accrual, our model clearly communicates the importance of the timeframe being considered for a policy choice to decision-

Table 2. Annualised cost of adopting a 5 per cent de-leaving threshold for yellow Sigatoka suppression in the NBPQA relative to a 15 per cent protocol aggregated across the region.

Description	15% de-leaving threshold (A)	5% de-leaving threshold (B)	B-A
Chemical treatment costs (\$ million)	115.4	146.1	31.3
De-leaving costs (\$ million)	19.6	32.0	12.5
Total (\$ million)	134.9	178.7	43.8

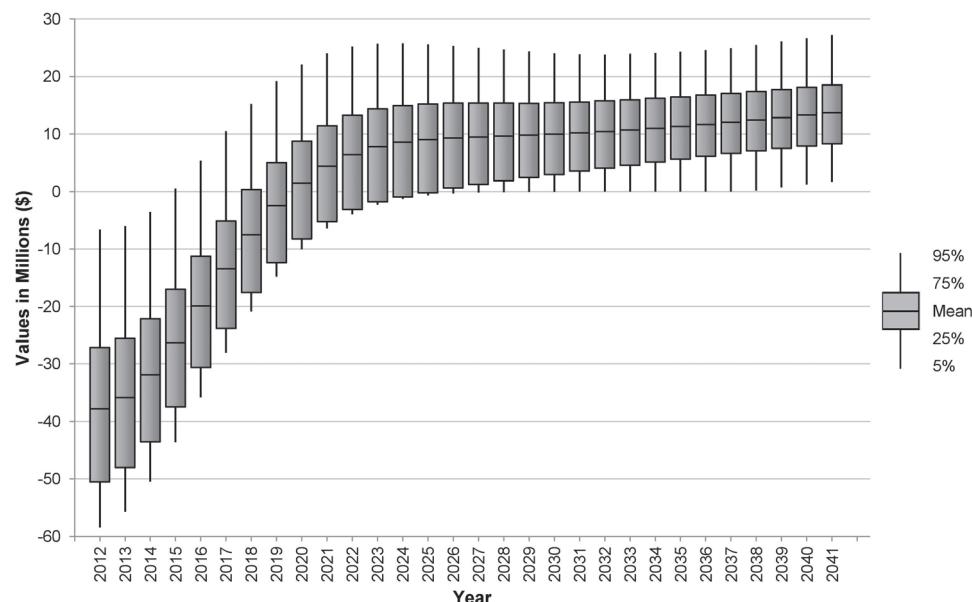


Figure 4. Predicted net benefit of adopting a 5 per cent de-leaving threshold for yellow Sigatoka suppression in the NBPQA relative to a 15 per cent protocol.

makers. Assuming they prefer to consider a 30-year time period, the annualised average present value of benefits expected to result from tightening the de-leaving threshold is likely to be small, but positive. Shorter time frames suggest the net benefits will be smaller, and (if less than a 10-year time frame is considered) possibly negative. We should also point out that if decision-makers apply a higher (personal) discount rate of 10 per cent to the mean or average model calculations, as opposed to a public/social discount rate of 5 per cent, the mean net benefit to the banana industry would fall to -\$1.6 million over 30 years. This highlights the importance of both the choice of time frame and the choice of discount rate.

While the modelling framework we have developed provides a solid foundation over which other comprehensive economic analyses of invasive species effects can be performed, future extensions to the model may be warranted in some situations. These could include the adoption of an ecosystems approach within the bioeconomic model to capture interactions between invasive and native species (Hulme 2006). It

may also be necessary to use more complex biophysical modelling of susceptibility and resilience to infection where polyphagous species are concerned (e.g. Hester and Cacho 2003). In these cases the importance of potential non-market (e.g. impacts on native biota, environmental costs due to the use of fungicides, etc.) and indirect market (e.g. impacts on input markets as industries are affected by invasive species) effects may also be critical factors that policy-makers wish to consider.

Conclusion

In a plant biosecurity context, it is often difficult to predict policy benefits over time due to complex biophysical interactions between invasive species, their hosts and the environment. In this paper, we have demonstrated how a bioeconomic analysis can help decision-makers using the example of *M. musicola*. We have developed an analytical approach using a stratified diffusion spread model to simulate the likely benefits of adopting a 5 per cent de-leaving threshold for *M. musicola* suppression in the NB-PQA relative to a 15 per cent protocol. Using Monte Carlo simulation to generate a range of possible incursion scenarios over a 30-year time period, we predict that in an average year this new protocol will only reduce the net impact of the disease by \$1.4 million. However, this result varies substantially depending on the timeframe over which benefits and costs are projected, with shorter time frames indicating poorer net returns from the change in protocols. Compounding this issue is the uncertainty involved in predicting policy impacts further into the future. It is therefore difficult to evaluate the 5 per cent de-leaving protocol. But, if we take the 30-year timeframe presented in our analysis as a guide, the effects of the policy are likely to be positive, but relatively minor.

Acknowledgements

The authors would like to acknowledge the support of the Australian Plant Biosecurity Cooperative Research Centre, established and supported under the Australian Government's Cooperative Research Centres Program. We would also like to thank two anonymous reviewers for their helpful comments on the paper.

References

- ABS (2012) Agricultural Commodities 2010–11, Australian Bureau of Statistics, Canberra, 36 pp.
- Acquaye AKA, Alston MJ, Hyunok ML, Sumner AD (2005) Economic consequences of invasive species policies in the presence of commodity programs: Theory and applica-

- tion to citrus canker. *Review of Agricultural Economics* 27: 498. doi: 10.1111/j.1467-9353.2005.00250.x
- Albers HJ, Fischer C, Sanchirico JN (2010) Invasive species management in a spatially heterogeneous world: Effects of uniform policies. *Resource and Energy Economics* 32: 483–499. doi: 10.1016/j.reseneeco.2010.04.001
- Barbier EB (2001) A note on the economics of biological invasions. *Ecological Economics* 39: 197–202. doi: 10.1016/S0921-8009(01)00239-7
- Born W, Rauschmayer F, Bräuer I (2005) Economic evaluation of biological invasions - a survey. *Ecological Economics* 55: 321–336. doi: 10.1016/j.ecolecon.2005.08.014
- Cacho OJ, Wise RM, Hester SM, Sinden JA (2008) Bioeconomic modeling for control of weeds in natural environments. *Ecological Economics* 65: 559–568. doi: 10.1016/j.ecolecon.2007.08.006
- Carrasco LR, Baker R, MacLeod A, Knight JD, Mumford JD (2010) Optimal and robust control of invasive alien species spreading in homogeneous landscapes. *Journal of the Royal Society Interface* 7: 529–540. doi: 10.1098/rsif.2009.0266
- Carrasco LR, Cook D, Baker R, MacLeod A, Knight JD, Mumford JD (2012) Towards the integration of spread and economic impacts of biological invasions in a landscape of learning and imitating agents. *Ecological Economics* 76: 95–103. doi: 10.1016/j.ecolecon.2012.02.009
- Colautti R, Bailey S, Overdijk CA, Amundsen K, MacIsaac H (2006) Characterised and projected costs of nonindigenous species in Canada. *Biological Invasions* 8: 45–59. doi: 10.1007/s10530-005-0236-y
- Commonwealth of Australia (2006) Handbook of Cost-Benefit Analysis. Department of Finance and Administration, Canberra, 180 pp.
- Cook DC (2003) Prioritising Exotic Pest Threats to Western Australian Plant Industries. Discussion Paper. Government of Western Australia - Department of Agriculture, Bunbury, 185 pp.
- Cook DC (2008) Benefit cost analysis of an import access request. *Food Policy* 33: 277–285. doi: 10.1016/j.foodpol.2007.09.002
- Cook DC, Carrasco LR, Paini DR, Fraser RW (2011a) Estimating the social welfare effects of New Zealand apple imports. *Australian Journal of Agricultural and Resource Economics* 55: 1–22. doi: 10.1111/j.1467-8489.2011.00558.x
- Cook DC, Fraser RW (2008) Trade and invasive species risk mitigation: Reconciling WTO compliance with maximising the gains from trade. *Food Policy* 33: 176–184. doi: 10.1016/j.foodpol.2007.07.001
- Cook DC, Fraser RW, Paini DR, Warden AC, Lonsdale WM, Barro PJD (2011b) Biosecurity and yield improvement technologies are strategic complements in the fight against food insecurity. *PLoS ONE* 6: e26084. doi: 10.1371/journal.pone.0026084
- Doak DF, Estes JA, Halpern BS, Jacob U, Lindberg DR, Lovvorn J, Monson DH, Tinker MT, Williams TM, Wootton JT, Carroll I, Emmerson M, Micheli F, Novak M (2008) Understanding and predicting ecological dynamics: Are major surprises inevitable? *Ecology* 89: 952–961. doi: 10.1890/07-0965.1

- Dwyer G (1992) On the spatial spread of insect pathogens - theory and experiment. *Ecology* 73: 479–494. doi: 10.2307/1940754
- Epachin-Niell RS, Hastings A (2010) Controlling established invaders: integrating economics and spread dynamics to determine optimal management. *Ecology Letters* 13: 528–541. doi: 10.1111/j.1461-0248.2010.01440.x
- Fisher RA (1937) The wave of advance of advantageous genes. *Annual Eugenics* 7: 353–369. doi: 10.1111/j.1469-1809.1937.tb02153.x
- Heikkila J, Peltola J (2004) Analysis of the Colorado potato beetle protection system in Finland. *Agricultural Economics* 31: 343–352. doi: 10.1111/j.1574-0862.2004.tb00271.x
- Henderson J, Pattemore JA, Porchun SC, Hayden HL, Brunschot SV, Grice KRE, Peterson RA, Thomas-Hall SR, Aitken EAB (2006) Black Sigatoka disease: new technologies to strengthen eradication strategies in Australia. *Australasian Plant Pathology* 35: 181–193. doi: 10.1071/AP06017
- Hengeveld B (1989) Dynamics of Biological Invasions. Chapman and Hall, London, 160 pp.
- Hester SM, Cacho O (2003) Modelling apple orchard systems. *Agricultural Systems* 77: 137–154. doi: 10.1016/S0308-521X(02)00106-3
- Holmes EE (1993) Are diffusion-models too simple - a comparison with telegraph models of invasion. *American Naturalist* 142: 779–795. doi: 10.1086/285572
- Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology* 43: 835–847. doi: 10.1111/j.1365-2664.2006.01227.x
- Hyder A, Leung B, Miao ZW (2008) Integrating Data, Biology, and Decision Models for Invasive Species Management: Application to Leafy Spurge (*Euphorbia esula*). *Ecology and Society* 13: 1–12.
- Lewis MA (1997) Variability, patchiness, and jump dispersal in the spread of an invading population. In: Tilman D, Kareiva P (Eds) *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton University Press, New Jersey, 46–74.
- McCann K, Hastings A, Harrison S, Wilson W (2000) Population outbreaks in a discrete world. *Theoretical Population Biology* 57: 97–108. doi: 10.1006/tpbi.1999.1444
- Moody ME, Mack RN (1988) Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* 25: 1009–1021. doi: 10.2307/2403762
- Naylor RL (2000) The economics of alien species invasions. In: Mooney HA, Hobbs RJ (Eds) *Invasive Species in a Changing World*. Island Press, Washington, D.C., 241–259.
- Okubo A, Levin SA (2002) Diffusion and ecological problems: modern perspectives. Springer, New York, 467 pp.
- Ostmark HE (1974) Economic Insect Pests of Bananas. *Annual Review of Entomology* 19: 161–176. doi: 10.1146/annurev.en.19.010174.001113
- Paarlberg PL, Lee JG, Seitzinger AH (2003) Measuring Welfare effects of an FMD Outbreak in the United States. *Journal of Agricultural and Applied Economics* 35: 53–65.
- Peterson R, Grice K, Goebel R (2005) Eradication of black leaf streak disease from banana growing areas in Australia. *InfoMusa* 14: 7–10.
- Rafoss T (2003) Spatial stochastic simulation offers potential as a quantitative method for pest risk analysis. *Risk Analysis* 23: 651–661. doi: 10.1111/1539-6924.00344

- Regan HM, Colyvan M, Burgman MA (2002) A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecological Applications* 12: 618–628. doi: 10.1890/1051-0761(2002)012[0618:ATATOU]2.0.CO;2
- Sanchirico J, Albers H, Fischer C, Coleman C (2010) Spatial Management of Invasive Species: Pathways and Policy Options. *Environmental and Resource Economics* 45: 517–535. doi: 10.1007/s10640-009-9326-0
- Sharov AA, Liebholt AM (1998) Bioeconomics of managing the spread of exotic pest species with barrier zones. *Ecological Applications* 8: 833–845. doi: 10.1111/j.0272-4332.2004.00486.x
- Shigesada N, Kawasaki K (1997) *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford, 205 pp.
- Simberloff D (2005) The politics of assessing risk for biological invasions: the USA as a case study. *Trends In Ecology & Evolution* 20: 216–222. doi: 10.1016/j.tree.2005.02.008
- State of Queensland (2003) Plant Protection Amendment Regulation (No. 4). Queensland Parliament, Brisbane, 27 pp.
- State of Queensland (2002) Plant Protection Regulation. Queensland Parliament, Brisbane, 171 pp.
- Ulubasoglu M, Mallick D, Wadud M, Hone P, Haszler H (2011) How price affects the demand for food in Australia - An analysis of domestic demand elasticities for rural marketing and policy. Rural Industries Research and Development Corporation, Canberra, 41 pp.
- Vose D (2008) *Risk Analysis: A Quantitative Guide*. John Wiley & Sons, Chichester, 752 pp.
- Waage JK, Fraser RW, Mumford JD, Cook DC, Wilby A (2005) A New Agenda for Biosecurity Horizon Scanning Programme. Department for Food, Environment and Rural Affairs, London, 198 pp.
- Wittwer G, McKirdy S, Wilson R (2005) Regional economic impacts of a plant disease incursion using a general equilibrium approach. *The Australian Journal of Agricultural and Resource Economics* 49: 75–89. doi: 10.1111/j.1467-8489.2005.00276.x
- Yemshanov D, Koch FH, McKenney DW, Downing MC, Sapiro F (2009) Mapping Invasive Species Risks with Stochastic Models: A Cross-Border United States-Canada Application for *Sirex nootilio* Fabricius. *Risk Analysis* 29: 868–864. doi: 10.1111/j.1539-6924.2009.01203.x

Prioritizing the risk of plant pests by clustering methods; self-organising maps, k-means and hierarchical clustering

Susan P. Worner¹, Muriel Gevrey², René Eschen³, Marc Kenis³, Dean Paini^{4,5},
Sunil Singh^{4,5}, Karl Suiter⁶, Michael J. Watts⁷

1 Bio-Protection Research Centre, PO Box 84, Lincoln University, Lincoln 7647 New Zealand **2** Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD 20688, USA **3** CABI, Rue des grillons 1, CH-2800 Delémont, Switzerland **4** Cooperative Research Centre for National Plant Biosecurity, Bruce, ACT 2601, Australia **5** CSIRO Ecosystem Sciences and Biosecurity Flagship, Black Mountain, ACT 2601, Australia **6** NSF Centre for Integrated Pest Management, North Carolina State University Raleigh, NC 27606 USA **7** Information Technology Programme, AIS St Helens, P.O. Box 2995, Auckland 1140, New Zealand

Corresponding author: Susan Worner (Worner@lincoln.ac.nz)

Academic editor: Trond Røfoss | Received 26 September 2012 | Accepted 4 July 2013 | Published 13 September 2013

Citation: Worner SP, Gevrey M, Eschen R, Kenis M, Paini D, Singh S, Suiter K, Watts MJ (2013) Prioritizing the risk of plant pests by clustering methods; self-organising maps, k-means and hierarchical clustering. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 83–102. doi: 10.3897/neobiota.18.4042

Abstract

For greater preparedness, pest risk assessors are required to prioritise long lists of pest species with potential to establish and cause significant impact in an endangered area. Such prioritization is often qualitative, subjective, and sometimes biased, relying mostly on expert and stakeholder consultation. In recent years, cluster based analyses have been used to investigate regional pest species assemblages or pest profiles to indicate the risk of new organism establishment. Such an approach is based on the premise that the co-occurrence of well-known global invasive pest species in a region is not random, and that the pest species profile or assemblage integrates complex functional relationships that are difficult to tease apart. In other words, the assemblage can help identify and prioritise species that pose a threat in a target region. A computational intelligence method called a Kohonen self-organizing map (SOM), a type of artificial neural network, was the first clustering method applied to analyse assemblages of invasive pests. The SOM is a well known dimension reduction and visualization method especially useful for high dimensional data that more conventional clustering methods may not analyse suitably. Like all clustering algorithms, the SOM can give details of clusters that identify regions with similar pest assemblages, possible donor and recipient regions. More important, however SOM connection weights that result from the analysis can be used to rank the strength of association of each species within each regional assemblage. Species with

high weights that are not already established in the target region are identified as high risk. However, the SOM analysis is only the first step in a process to assess risk to be used alongside or incorporated within other measures. Here we illustrate the application of SOM analyses in a range of contexts in invasive species risk assessment, and discuss other clustering methods such as *k*-means, hierarchical clustering and the incorporation of the SOM analysis into criteria based approaches to assess pest risk.

Keywords

Invasive pest assemblages, prioritisation, self-organising maps, hierarchical clustering, *k*-means, multi-criteria analysis, plant pathogens

Introduction

Global tourism, trade and climate change continue to drive invasive species impact by increasing opportunities for species dispersal and establishment in new regions of the world. Nonindigenous invertebrates, vertebrates, plants, bacteria, fungi and viruses continue to establish in regions where they are not normally found (Vitousek et al. 1997), threatening both cultivated and indigenous species. Invasive species are capable of doing irreparable damage to the biodiversity of natural and agricultural ecosystems and to human and animal health, but for many nations, protecting the biological potential and production of managed systems is of particular concern, as well as increasingly urgent, as climate change threatens global food security. For greater preparedness and prevention, important decisions about invasive species need to be supported by a range of approaches that are integrative and capable of converting scientifically relevant data into data that is also decision relevant.

Regulators and pest risk assessors face the unenviable task of providing pest lists to policy makers based on their assessment of risk of pest establishment in endangered areas. When creating such lists it is difficult to ignore species that have a recent history of invasiveness. The result can be compilations that are often qualitative, subjective and frequently biased toward current knowledge and expertise of the panel involved in the creation process. Despite such drawbacks, regulators use such lists to allocate scarce resources to the prevention of perceived high risk species establishing.

Many attempts have been made to address the shortcomings of pest prioritisation but few have delivered anything that approaches a rigorous quantitative process. For example, a range of tools for prioritisation can be found in plant risk management (see Skurka Darin et al. 2011 for a brief review). Very few new tools have centred on arthropod pests or plant pathogens. Trait-based categorisation of invasive pests that aspire to give some predictive capability have been attempted with little success. For example, a study by Simberloff (1989) attempted to characterise the traits that lead to successful establishment of insects. As well, Peacock and Worner (2008) compared a selection of insect species that are often intercepted at the New Zealand border that have established, with species that, despite numerous interceptions over many years, have not yet established. The latter were used as a proxy for “failed” introductions. More recently,

Philibert et al. (2011) used species-level traits of forest pathogenic fungi to predict invasion success using a combination of ecological and biological traits.

However, data associated with invasive species, as for most ecological data, involve features that are complex, dynamic and nonlinear. Many conventional multivariate statistical approaches used to analyse such data often involve linear methods that are affected by noise and outliers (Chon 2011). The purpose of this study is to review the use of the co-occurrence of pest species that make up regional species assemblages or profiles for knowledge discovery. We also review the application of novel nonlinear methods such as a neural network called Kohonen self-organising map (SOM) (Kohonen 1982) and other clustering methods, to the problem of prioritising pest species by profiling pest assemblages in target regions. Additionally, future research requirements if such methods are to be used to influence policy decisions, will be highlighted.

The idea of clustering pest complexes or assemblages of species to identify donor and recipient regions in an invasive species context was described by Worner and Gevrey (2006) using a self-organising feature map. Using species assemblages as indicators of environmental conditions is not new. Assemblages of fossil organisms such as Radiolaria and Foraminifera are used in petroleum geology and oil exploration to indicate presence of fossil hydrocarbon reservoirs (Gregory et al. 2007) as well as past climates (Heiri and Lotter 2005). Species assemblages are also well used in fresh water studies and other ecosystem studies to determine changes in composition or behaviour in response to toxic substances and responses to natural and other anthropocentric changes (Chon 2011, Lek and Guégan 2000). A SOM is an artificial neural network that can detect patterns and similarity in complex data. SOMs have found application in a range of disciplines from image recognition (see Chon 2011 for a short review) to detecting shifts in climate (Schmidt et al. 2012).

A basic assumption underpinning the Worner and Gevrey (2006) and Gevrey et al. (2006) studies is that a grouping or assemblage of pest species integrates complex variables that are difficult to tease apart. Some might question that assumption on the basis that such groupings are not natural and have come about mainly by anthropogenic influences. Despite that a history of transport, trade and food production has largely influenced which pests are where in the world, it is clear that those species able to establish viable populations rely on a complex interaction of biotic and abiotic variables. Indeed, Watts and Worner (2009a) have shown that such pest groupings are not random assemblages of species. Co-occurrence of species forming a particular pest profile for a region indicates suitable environmental conditions, and in the case of arthropod pests and plant pathogens, co-occurrence indicates suitable hosts and a particular invasion history of the region. In their 2006 study, Worner and Gevrey first used a conventional cluster analysis to identify global donor and recipient regions, using more than 800 species over 456 geopolitical areas (Worner and Gevrey 2006). The analysis resulted in long drawn out clusters that were difficult to interpret. They then applied a self-organising map (SOM) that appeared to have a number of advantages. The first is that the high dimensional data set was reduced to a 2-dimensional map or visualisation that greatly improved interpretation (Fig. 1). In addition, the analysis created a separate map for each species in the assemblage with a weight

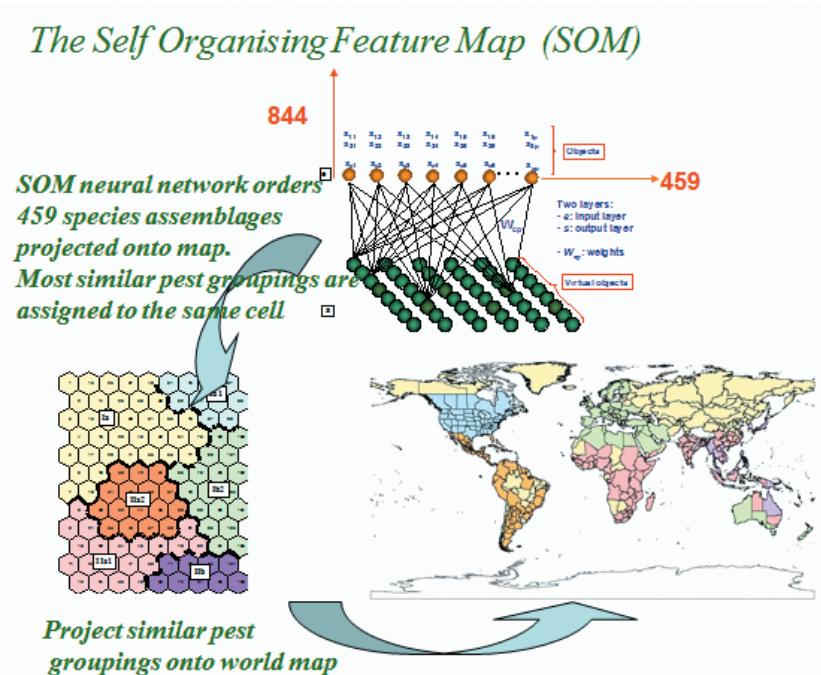


Figure 1. A representation of the application of a self organising feature map to the analysis of pest distribution data.

or value that indicated the strength of association that species has for the pest profiles or assemblages associated with the cells in the map. These weights allow the species complex for a region to be filtered into high risk established species and high and low risk non-established species. The high weight allocation for a species in a region indicates it is closely associated with the particular pest complex of that region. In other words, the species co-occurs globally with similar assemblages of pests. For species that are not established but allocated a high weight, the weight is interpreted as an index of high risk of establishment.

Clearly, clustering can be done using a number of approaches and SOM clustering can be used in a number of contexts to address the problem of pest risk assessment. We discuss some recent studies that further explore SOM analysis or are variations of that approach, along with some alternative clustering methods in more detail.

Clustering methods and applications to risk analysis

Data

The data used in all the studies reviewed here comprised the presence and absence of pest species in different countries and regions in the world. This information was extracted with permission from the CABI Crop Protection Compendium (2003, 2007)

and CABI's Plantwise Knowledge Bank (<http://www.plantwise.org/knowledgebank>), which are interactive multimedia encyclopaedias edited by CABI, a not-for-profit science-based development and information organization.

Data presented by country or geographical regions where pest presence or absence is represented by binary data, with 0 corresponding to absence and 1 corresponding to presence of species in a specific geographical area. Incomplete data from the database were discarded. Depending on the taxa of interest in the study, different numbers of pest species and regions comprised the actual database used for analysis.

The SOM Model

A detailed description of self-organising maps (SOM) can be found in Kohonen (1982) and Kohonen (2001), and examples of its application to pest risk data in Worner and Gevrey (2006) as well as Gevrey et al. (2006). The self-organising map is an unsupervised learning algorithm that is a type of neural network. A SOM consists of two layers of artificial neurons, 1) the input layer that represents the input data (pest profiles comprising, presence = 1 or absence = 0 for each species in each region) and the output layer or map, which is usually arranged in a two-dimensional structure (Fig.1). Every input neuron or vector (pest profile) is connected to every output neuron (map neuron or node), and each connection has a weight attached to it. The batch SOM algorithm can be summarized as follows: (i) Initialize the values of the virtual (node) vectors (VV_i , $1 \leq i \leq c$) using random values. (ii) Repeat steps (iii) to (vi) until convergence. (iii) Read all the sample vectors (SV or pest profiles) one at a time. (iv) Compute the Euclidean distance between SV and VV . (v) Assign each SV to the nearest VV according to the distance results. (vi) Modify each VV with the mean of the SV that were assigned to it (Worner and Gevrey 2006). In other words, when the input vectors (pest profiles for global sites) are presented to the SOM algorithm, random weight values are assigned to each virtual (weight) vector associated with each neuron (node) of the map. For each input vector (pest profile) the Euclidean distance between the input vector (pest profile) and the incoming weight (node or virtual) vector of each map neuron, is calculated. Each input vector is then assigned to the closest virtual vector (the winner, also known as the best matching unit (BMU)) according to the Euclidean distance. Each virtual vector is then updated during an iterative learning process, where weights are modified according to equation (1.1).

$$w_{i,j}(t+1) = w_{i,j}(t) + h(t)(x_i - w_{i,j}(t)) \quad (1.1)$$

where $w_{i,j}(t)$ is the connection weight from input i to map neuron j at time t , x_i is element i of input vector x , and h is the neighbourhood function. In other words, the neighbourhood function determines how strongly the neurons or nodes are connected to each other, as defined in equation (2).

$$h(t) = \alpha \exp(-d^2/(2\sigma^2(t))) \quad (1.2)$$

where α is the learning rate, which decays towards zero as time progresses, d is the Euclidean distance between the winning unit (BMU) and the current unit j , and σ is the neighbourhood width parameter, which also decays towards zero (Watts and Worner 2009b).

Basically, the large number of data vectors, or pest profiles are sorted such that those pest profiles that are most similar are associated with a particular node, neuron or cell on the map. Additionally, pest profiles associated with cells that are close to each other are more similar than those cells that are further away. While the SOM algorithm is essentially a clustering algorithm, the detail within each cluster is very useful for questions concerning the invasive species of interest. The analysis shows similarities between pest profiles of countries and regions despite that intuitively many regions may not appear to have analogous climates and environmental conditions. Clearly, however, such similarity requires close study and indeed, if the percentage similarity between any two countries in a cluster is examined one usually finds a level of similarity that is often unexpected. Clearly, the SOM analysis is only the start of a more detailed analysis into what the clusters mean. The most important result of the SOM analysis is that the SOM weights can be used to create a risk list where the weight assigned to each species (element in the vector of species) can be used as an index of the risk of those species of establishing in the target area Gevrey et al. (2006). In this way, a subset of the original 844 species can be targeted for more in-depth risk assessment.

Sensitivity analysis of SOMs

Databases often contain errors and the concern is that such error will significantly affect the confidence in any analysis that is based on the database. Paini et al. (2010a) evaluated the sensitivity of the SOM method by altering the original presence/absence data by an increasing percentage and compared estimates of risk with those generated by a national coordinating body (Plant Health Australia) utilizing expert stakeholder opinion. The same species distribution data set as used by Worner and Gevrey (2006), described above, was used in this study. Additionally, Impact Risk Assessments (IRAs) generated by the Australian Government's Department of Agriculture, Forestry, and Fisheries (<http://www.daff.gov.au/ba/ira/final-plant>) were analysed to estimate the error rate in a sample of the CABI data and to determine the range of data alteration required. To simulate database error, data from all regions in the original database (459) were altered by 5%, 10%, 20%, and 30%. To do that, a set percentage of species were randomly selected from each regional pest profile and their presence or absence records reversed. Each region was altered separately so that no two regions were altered in the same way. Paini et al. (2010a) found that evaluation of the risk posed by the species based on the SOM analysis remained unaffected by alterations of up to 20% of data over all regions (Fig. 2). Of interest was the comparison of species indicated as high risk by the SOM with expert stakeholder methodology. Unsurprisingly, the comparison revealed significant differences in the estimates of establishment risk.

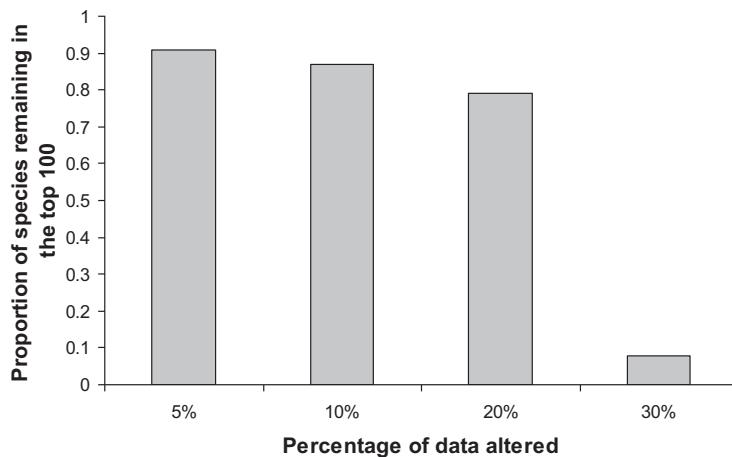


Figure 2. The proportion of species remaining in the top 100 list in response to an increasing level of data alteration. (Reprinted with permission from Paini et al. 2010a).

Clearly, no data set is complete and the impact of potentially inaccurate or incomplete data was tested in another study where species profiles were bootstrapped (resampling with replacement) 1000 times and the change in each species rank (highest weight to the lowest) was recorded (Watts and Worner 2009b). The New Zealand regional pest profile was used. For the top 50 most highly ranked species, that were not established in New Zealand, their ranks changed on average only 14 places out of a possible 800, indicating considerable confidence in the method.

SOM Validation: New Zealand data

Another question is whether a SOM analysis could have helped identify those pest species that actually established in a target region. As a means of validation Worner and Soquet (2010) carried out a new SOM analysis on an updated CABI data base (CABI 2007). New Zealand's pest profile again was used where the status of each currently established pest species was changed one at a time. In other words, if a species is established/present (1) its status was changed to not established/absent (0). The objective was to determine whether changing a species status from present to absent changes its risk index significantly. After the status of a single species was changed from present to absent, a new self-organizing map was created using the modified data and the new risk index for the target species recorded. Following that, the species status was reinstated to its original before repeating the process with the next established/present species.

By using the same initial parameters for a SOM (map size, initial weight values, number of epochs), the same clusters were formed and for each trial, the same regions were associated with the same neuron or node (cell on the map).

A rank was also associated with each species depending on its weight or risk value. Before validation the species were sorted in descending order from the species with the highest risk allocated the first rank and so on. Using ranks is a good way to measure the change in the risk by evaluating the change of rank before and after alteration. If a species rank hardly changes, in other words, if a previously present species that is changed to absent, maintains a high rank or risk index on re-analysis of the data then the self-organizing map has performed well.

The Spearman's rank correlation between ranks obtained before and after data modification was $r = 0.987$, showing high correlation. Altering the data did not have a significant influence on risk assessment. A species that is highly ranked remains highly ranked even though its status is changed. Notably, the cluster to which New Zealand was assigned also never changed, nor were the adjacent neurons modified. Those results once again, illustrated the stability of the method.

The average change in risk values for the top 100 pests was 0.07 and the ranks changed on average, 14 places (Fig. 2) for the 120 established species when their status was changed to absent (Worner and Soquet 2010). Clearly, their initial high risk index barely changed after data transformation thus a SOM analysis would have identified these species as high risk before they established in New Zealand. Despite this, a change of status of 4 of the 120 species currently present in New Zealand resulted in a

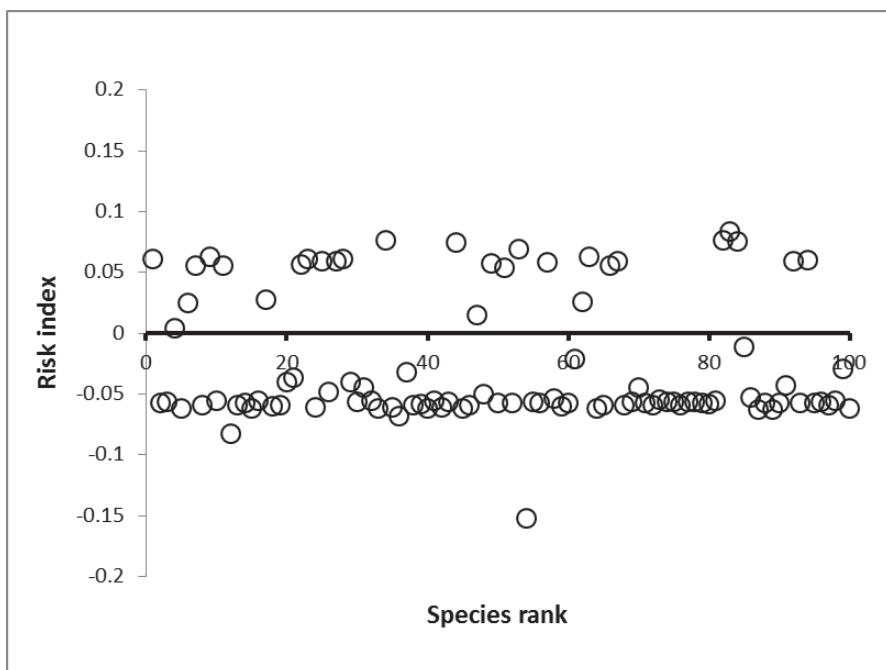


Figure 3. Average absolute change in risk index = 0.07.

change of cluster. For these 4 species the risks values also changed considerably. Some species have low initial risk simply because of low prevalence. Any interpretation of risk for low prevalence species, in other words less than about 20 occurrences, requires much caution and should be based on additional information. It is clear however that this tool is robust enough to not be influenced by even quite large variations for a large number of known global crop pests.

SOM Validation: USA data

Suiter (2011) carried out a SOM analysis on USA data. The data bases used were the Global Pest and Disease Database (GPDD) which is an archive of information for pests of concern to the USA. The study also used data extracted from the CABI Crop Protection Compendium (CPC) as described above for comparative analysis. The GPDD comprised over 3000 species and is well used by many agencies such as the United States Department of Agriculture (USDA), Customs and Border Protection (CBP), Department of Homeland Security (DHS) and State Co-operators. In contrast to the study carried out by Worner and Gevrey (2006) and Gevrey et al. (2006), Suiter (2011) included all pest species recorded in the respective data bases, from bacteria to weeds, in the analysis. World pest distribution data extracted from both databases included only distributions marked as "Present". "Unverified, Uncertain, Eradicated, Intercepted" and "Questionable" citations were discarded. The resulting analysis of the GPDD data comprised 45,051 unique distribution records and for the CABI database, there were 47,411 unique distribution records. Interestingly, there was only 9.8% overlap in the species recorded in each database (Fig. 4). Of particular interest with respect to validation of the SOM method was the number of high risk species, as determined by the SOM method, that were not established in 2007, that subsequently established by 2011. A 10 X 15 SOM map was used for the analysis and the databases were analysed separately.

The analysis of the GPDD database showed six species with high risk indices that had not established in 2007 had established by 2011 and also six species with high risk indices in the CABI database. These species were not the same, so 12 high risk species have subsequently established by 2011. It is not known whether any of these species were regulated at the time or whether they were on any agency risk list. It appears that the SOM analysis is a useful filter that may alert risk assessors to potential threats that require a closer analysis.

Suiter (2011) found that the SOM analysis was quite robust and provided a consistent fit of the neural network to the pest distribution data. Suiter (2011) pointed out that the results of the analysis may be subject to data over- or under-sampling artefacts. For example, countries that have been heavily sampled for invasive pests (i.e., USA, China, Australia) consistently cluster together on the SOM neural net. Suiter (2011) concluded that this could be due to one or more of several factors, 1) a high probability of overlap in pest assemblages for countries with a large number of pests,

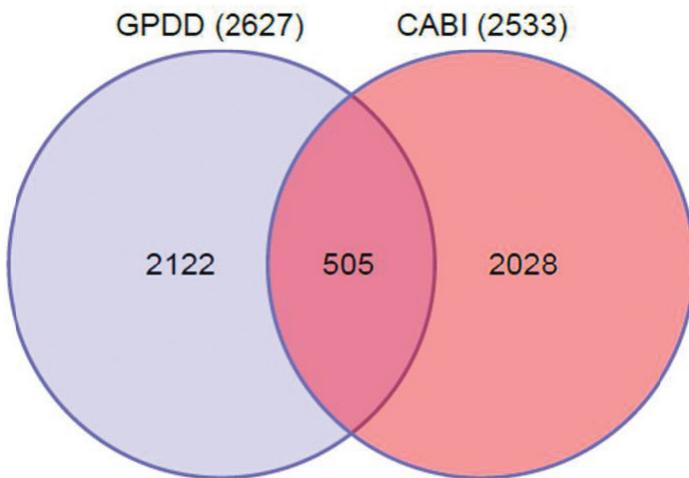


Figure 4. The level of similarity between the GPDD and CABI databases.

2) the countries are vast with a wide range of climates that may be very similar, 3) the countries with high pest numbers may be major trading partners and the similarities in current pest assemblages are most likely historical in nature due to trade and human movement, and 4) these countries have the resources and capacity to survey for invasive pests, unlike poorer countries. However, comparing the results of Suiter (2011) with the findings of Worner and Gevrey (2006) it appears that oversampling does not completely explain why some clusters occur. For example, Worner and Gevrey (2006) found that some countries (e.g., Tasmania, 63 species) in the New Zealand cluster had only half the number of species as some other countries (Canary Islands, 125) in the same cluster. Also the fact that trading history is important has always been proposed as one of the reasons why some pest assemblages are similar (Worner and Gevrey 2006, Paini et al. 2010b).

The Suiter (2011) study found that of the 2600 GPDD pests and 2500 CABI pests, only 505 (9.8%) (Fig. 4) were shared by both datasets and despite that, the GPDD and CABI geopolitical SOM projections looked very similar. When risk rankings were used to produce a prioritized pest list, the species compositions generated for the United States for both datasets were quite different. The study illustrates that the composition of the pest species complex present in a dataset and the distribution of species in the country of interest, are important. When there are many endemic pests in the data matrix for a large area like USA, the Euclidean distance values (risk ratings) for pests tend to be significantly lower in general than if the majority of species in the pest profile are not present in the country. That result highlights the need to analyse and interpret the results of each database separately and be mindful of endemic species that may have very low global prevalence and therefore tend not to co-occur with many other species. The fact that each database was able to highlight the risk of

a number of species that had not established in 2007 but subsequently established by 2011 (Suiter 2011), illustrates that the information in each database, despite being different, is valid.

SOM Validation: simulated data

Paini et al. (2011) tested the ability of the SOM to rank fungal species that could establish in a region above those species that couldn't establish according to simulated data. The authors did this in a virtual world in which regions had particular characteristics and species had particular requirements. Surprisingly, there was little or no difference between species that had low prevalence and species that were widely distributed and the success rate was above 90% for all species.

K-means clustering

K-means is an unsupervised algorithm that performs clustering (Lloyd 1982). In other words, the algorithm finds the best way to partition data into groups or clusters. The name *k*-means comes from the fact that the user decides how many clusters (*k* clusters) are necessary to partition data. The *k*-means algorithm proceeds as follows:

Choose *k* initial centres. These centres (vectors) can be generated randomly or they can be vectors that are randomly selected from the data set.

For each data vector (eg. regional pest profile), calculate the distance to each of the *k* cluster centres.

Assign each data vector (pest profile) to its nearest cluster.

Calculate new cluster centres, corresponding to the mean of all vectors in each cluster.

Repeat steps 2-4 until a stopping condition is reached. This is usually when vectors no longer change the cluster they are assigned to, that is, the clusters are stable.

The approach of using *k*-means to analyse the regional pest profiles is the same as the self-organizing one where geographical regions are clustered together based on their pest species assemblage (pest profiles) to determine which species are more likely to establish in a new region. In *k*-means, the risk index of a species establishing in a specific region is assessed by its frequency of presence in the vectors/pest profiles in the cluster to which the target region has been assigned. Watts and Worner (2009a, 2009b, 2011, 2012) have reported a number of analyses of the CABI data set (2003, 2007) described above, using *k*-means clustering. In Watts and Worner (2009b) the results of clustering insect assemblages with SOM were compared with the results of the *k*-means algorithm. While that study found that in some ways *k*-means could be superior to SOM, several issues were left unaddressed such as the effect of noise or small random changes to the performance of each algorithm.

Watts and Worner (2012) compared the performance of SOM maps with the performance of equivalent k -means algorithms over assemblages of bacterial crop diseases and also investigated the effects of adding noise to the assemblages and measuring cluster quality. Cluster quality for each algorithm was measured using quantisation error (Hansen and Jaumard 1997), which is the mean distance between each vector and the centre of its cluster. In addition, the computational efficiency of each algorithm was also considered. While the Watts and Worner (2012) study found differences in the performance of the clustering algorithms in most instances the difference are not significant. More important, however, in this study as well as previous studies, the different algorithms give high to medium risk indices to basically the same species. For example, in the Watts and Worner (2012) study only 12 species out of the top 80 used for the comparisons, were not in both the SOM and k -means risk lists.

Hierarchical clustering

Borgatti (1994) and Hastie et al. (2009) give good explanations of hierarchical clustering as a means of classifying similar samples or objects. Given a set of N items to be clustered, the start of the hierarchical agglomerative clustering is to:

Assign each item to its own cluster. In each of the subsequent steps, two clusters are merged and a new cluster is formed until all clusters are merged into a single cluster. There are various methods to determine which clusters are merged, for example using the most similar pair of observations in two clusters (single linkage), the most dissimilar pair of observations (complete linkage) or the dissimilarity between the average of the observations in each cluster (group average; Hastie et al. 2009). The method used to merge clusters determines the size of the clusters and the relationships between them. A dendrogram provides a graphical representation of the relationship between the clustered items by plotting each merge at the similarity (distance) between the merged groups. It is important to note that, like the other clustering techniques discussed in this paper the clustering result does not imply a causal relationship and should be interpreted with caution.

An example of a hierarchical cluster analysis of the CABI data is provided by Eschen and Kenis (2012) who investigated the trade in woody plants for planting in Europe, as a major pathway for the introduction of alien forest pests and diseases. While phytosanitary inspections at the import stage are essential to prevent such introductions, Eschen and Kenis (2012) suggest they are limited and tend to target recognised pests, particular hosts and shipments that are likely to contain them. Such phytosanitary inspections tend to be biased, moreover, the identification of risk depends to some extent on expert judgement. The aim of the Eschen and Kenis (2012) analysis was to provide an objective assessment of the risk posed by individual species and identification or prediction of potential sources of invasive species based on the global distribution of known pests. Eschen and Kenis (2012) analysed distribution data (presence/absence data) obtained from CABI's Plantwise Knowledge Bank (<http://www.plantwise.org>)

wise.org/knowledgebank) for 1009 invertebrate pests and pathogens of woody hosts in 351 global regions within 183 countries. Seven large countries were subdivided into regions. The 1009 taxa were divided into twelve groups (4 micro-organism and 8 invertebrate taxa).

Countries and regions with similar pest species assemblages were identified for each organism group using hierarchical cluster analysis and the likelihood of establishment of those species was calculated as the proportion or frequency of countries within the cluster containing EU and European Free Trade Association countries (EFTA) where each species has been recorded as present. Taxa recorded in fewer than six regions were excluded from the analysis to reduce the influence of rare species and outliers. Eschen and Kenis (2012) used Ward minimum variance method (Ward 1963) to determine which clusters were merged, as it consistently produced interpretable clusters, while other methods did not. The optimal number of clusters was determined for each of the twelve groups of taxa using the Davies-Bouldin Index, a measure based on the ratio between the variation within and between clusters (Davies and Bouldin 1979).

Interpretable clusters were formed for all groups of taxa, except for the Oomycetes, where the European countries were spread over all clusters. Clusters for micro-organisms contained nearly twice as many regions as clusters for invertebrates (111 vs. 61 regions per cluster). The non-EU regions with the most similar pest species assemblages to EU regions were North America, the Mediterranean region, the northern part of Eurasia and Australia/New Zealand (Fig. 5), which have a broadly similar climatic range as the EU and a long history of intensive trade. Most pest species in the database

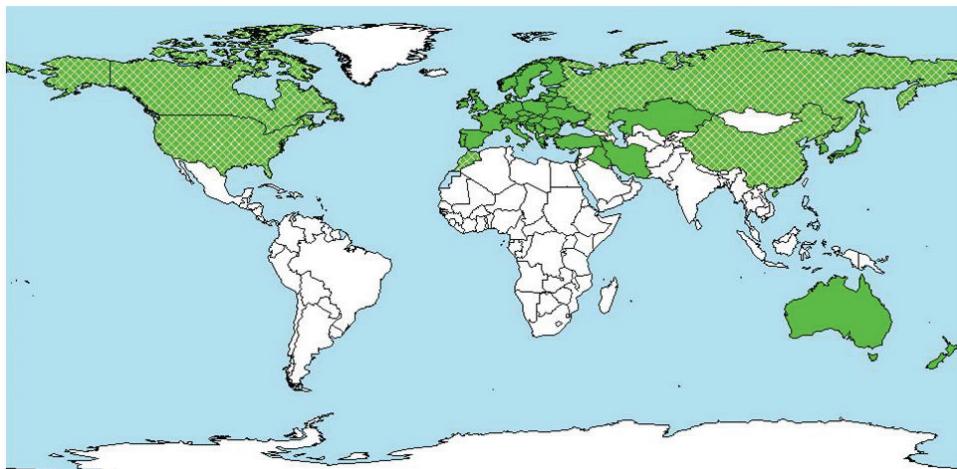


Figure 5. Geographical representation of the results of the hierarchical cluster analysis for species of micro-organisms and invertebrates. Countries on the map that are hatched have several regions that typically are in the European cluster. For each country and organism group, lists were produced that indicate those species that pose the greatest risk.

used for hierarchical analysis were already present in one or more EU countries at the time of the study, which indicated that the risk of these species primarily comes from within the EU and is similar to the result of Paini et al. (2010b), who used a SOM to identify potential new invasive agricultural invertebrate pests for the USA and also found that the majority of species in their dataset were already recorded in one or more states. Moreover, the high proportion of species already recorded in the target region lowered the risk values (Suiter 2011). Eschen and Kenis (2012) suggested that combining the results of this analysis with economic data could provide a clearer indication about the likely origin of unidentified, future alien species establishing in Europe, that should be considered when assessing the risks associated with the import of woody plants for planting.

SOMs and multi-criteria analysis

Plant-parasitic nematodes (PPN) cause estimated losses of \$157 billion/year worldwide (Abad et al. 2008) and documented losses of \$600 million/year in Australia (Hodda 2009). Fortunately, Australia does not have many of the globally damaging and quarantinable PPN species and the current losses result from the activities of a relatively few damaging species, such as root-knot nematodes, root lesion nematodes, cereal cyst nematode, *Heterodera avenae* and potato cyst nematode, *Globodera rostochiensis* (in the state of Victoria only). Despite this, trade is increasing, as it is in many other countries, thus providing multiple pathways for introduction of more exotic nematode species. Based on the need for a system to prioritize risks from many PPN species and to predict their potential biosecurity threats, Singh et al. (2012) carried out a study that analysed the distribution data of 250 PPN species from 355 regions worldwide using a SOM. As in the previous studies, Singh et al. (2012) compared the presence and absence of pest species in Australia to other regions of the world by clustering regions with species assemblages similar to Australia and her component states. The SOM was also used to determine regions which could act as a donor for potential invasive species.

Singh et al. (2012) considered that in addition to distribution, there are other criteria that contribute towards the risks and impact of a species. Additionally, there are often biases in the distribution data as thorough nematode surveys are lacking in countries where there is very limited nematological expertise available. In consideration of all these factors, Singh et al. (2012) devised an assessment including the following nine criteria. For example, 1) the existence of particular pathways, 2) survival adaptations, 3) pathogenicity, 4) host range, 5) whether the species is an emerging pest, 6) its taxonomy, 7) the existence of particular pathotypes and, 8) association in disease complexes, and, 9) the level of knowledge that exists about the species. For each of the nine criteria, a probability scale was established indicating the level of risk. For example, for the pine wilt nematode, *Bursaphelenchus xylophilus*, and the criterion “Pathways”, they define the probability scale as, a) association with propagative material $p \geq 0.6$, b) association as a contaminant, $p < 0.6 > 0.3$, c) not directly associated with trade $p < 0.3$. For each

criterion, probability values were estimated based on both literature search and expert judgment. Following that, weights were assigned based on the relative contribution of each criterion towards the biosecurity risk. The SOM index from the analysis of PPN distributions was combined with the values from the nine criteria and the sum of the weighted average values was calculated to determine the overall biosecurity risk.

Initial SOM clustering indicated that potential donor regions or regions from where species are most likely to pose the greatest threat were unsurprisingly, Australia's major trading partners. *Bursaphelenchus xylophilus* is a well known quarantine nematode species and based on the SOM analysis of the distribution data the resulting SOM index of 0.37 indicated the species to be of medium risk. Singh et al. (2012) used SOM index risk scale, > 0.7 = High, < 0.7 > 0.3 = Medium and < 0.3 = Low risk. When the criteria based assessment was included, the resulting risk value was much higher than that estimated by the SOM index alone (Table 1).

The higher risk is the result of considering the potential economic impacts of the species and additional information such as recent spread and availability of pathways as indicated by the number of interceptions in wood packaging materials and pine timber products. Another example is the carrot cyst nematode, *Heterodera carotae*, an economically important pest which currently has a restricted distribution. However, despite this restricted distribution, there is evidence of its spread and also its good survival adaptations by the formation of cysts. The SOM estimate ranked the species as low risk, but based on the multicriteria analysis, it becomes categorised as a medium risk species (Table 2).

The study by Singh et al. (2012) illustrates, as Worner and Gevrey (2006) suggested, that relying only on SOM estimates alone may lead to under- or overestimation of risks depending on the species. SOM remains a useful method for initial prioritization and can be incorporated with criteria based methods to better estimate a species biosecurity risks. A similar suggestion was made by Eschen and Kenis (2012), who found that their analysis did not identify Asia as a potentially important source or donor region for new invasive pests, despite a recent, strong increase in trade in plants for planting from that region.

Table I. SOM analysis and criteria based assessment of the pine wilt nematode (*B. xylophilus*)

Criteria	Probability	Weight
Distribution (SOM index from 1)	0.37	0.2
Pathways	0.80	0.15
Survival adaptations	0.65	0.1
Pathogenicity	0.85	0.1
Host range	0.55	0.1
Emerging pest	0.80	0.1
Taxonomy	0.60	0.1
Pathotypes	0.50	0.05
Disease complex	0.60	0.05
Knowledge	0.45	0.05
Sum (probability by weight)		0.62

Table 2. The results of a multi-criteria analysis for a range of exotic nematode species.

Species	SOM Index	Combined weighted average
<i>B. xylophilus</i>	0.37	0.62
<i>H. carotae</i>	0.10	0.47
<i>H. glycines</i>	0.40	0.63
<i>H. oryzae</i>	0.47	0.52
<i>M. chitwoodi</i>	0.20	0.62

Discussion

The studies described here suggest that SOMs can provide additional or preliminary information for evaluation and prioritisation of alien invasive species. It appears that no matter which clustering method or database is used, the analysis of similarities among pest species assemblages or regional profiles can be very useful. A criticism made by stakeholders has been that the databases used for such analyses contain a substantial number of errors. However, sensitivity analyses carried out by Paini et al. (2010a) and Watts and Worner (2009b) show that species weights and species ranks appear relatively robust to quite large errors in species distribution data. Given the many errors of omission and commission that are inevitable in such databases, these findings illustrate the practical utility of this approach and the utility of SOMs as a method, that can complement the current approaches used by biosecurity agencies. Additionally, the study by Suiter (2011) showed that quite different databases can still provide useful assessments of potential threats borne out by the number of species in each database given high risk weightings in 2007 that eventually established by 2011. In addition, the Suiter (2011) study seems to indicate that there may be some value in including other pest taxa in the analysis. The reason why the inclusion of more pest species might give better results is that more species may better characterise the pest complex by integrating more information about the abiotic and biotic influences of the region compared with fewer species. This hypothesis clearly requires more research.

With respect to the clustering methods that have been applied to the pest prioritisation problem, they all have advantages and disadvantages. The SOM analysis is computationally less efficient, but gives rich results. *K*-means is reputed to be susceptible to outliers and the results greatly depend on the initial partitions (the values of the cluster centres). However, an advantage of a SOM analysis is that it deals quite well with outliers. Indeed we have observed it can confine outliers in a part of the SOM map without affecting the other parts. *K*-means just partitions the data, whereas a SOM analysis preserves the relationship between neighbouring clusters or nodes in the map. Nearby data vectors in the input space are mapped onto neighbouring locations on the output (map) thereby preserving the internal structure of that data. SOMs also provide good data visualization and provide users with results that can simplify further analysis.

Despite the difference between SOMs and *k*-means, a further analysis of the results in Watts and Worner (2012) shows that the differences between a *k*-means analysis and

a SOM analysis can be minor if the same number of clusters as the SOM analysis are used. The advantage of *k*-means over SOM is that it is much more computationally efficient, however that does not seem so important when risk analyses, particularly when related to a new commodity or import risk assessment, may take a year or more to complete.

A striking feature when the clusters that result from the methods presented here are compared is the similarity of the results. The clusters in Worner and Gevrey (2006), Watts and Worner (2009b), Eschen and Kenis (2012) and another study by Vänninen et al. (2011) are very similar, although three techniques and two different datasets were used. The Eschen and Kenis (2012) study investigated twelve groups of invertebrates and micro-organisms with woody hosts, while the other studies investigated agricultural insect pests, but the clusters produced were strikingly similar. Such similarity suggests that the results of all three techniques were robust. However, values for the risk factors varies and a formal comparison of the methods discussed here would be desirable.

Like all data analyses, the methods described here involve error. A weakness of all the clustering methods is their inability to provide a realistic risk index for species that have a restricted distribution and low prevalence, or emerging pests that initially have low prevalence and therefore low co-occurrence with other species. Although Paini et al. (2011) showed the SOM was able to successfully identify even low prevalence species as having a higher likelihood of establishing than other more widespread species that were not able to establish. The SOM method in particular identifies species that are strongly associated with a particular pest profile. For those species that are not yet established, there could be very good reasons why those species have not established but clearly they need closer study. Other information should be considered. In fact the multi-criteria analysis is a good example of first using the SOM analysis to target species for in-depth risk assessment then quantifying additional relevant information to provide a more informed risk assessment.

Recommendations

Self-organising maps and other clustering methods have been used to filter the large amounts of information about the distribution of known global invasive arthropod pests and plant pathogens for risk assessment to help prioritise policy and resources. This novel approach continues to be researched and adopted by a scientists and agencies internationally to provide decision support for risk assessors. With more people applying the concept of clustering invasive species assemblages, indicative protocols that allow for robust comparative studies need to be developed. Protocols for the detection and removal of possible outliers, guidance for the choice of the initial number of seed clusters (or cells for a SOM), acceptable methods for cluster validation and judging cluster quality across all methods as well as methods for reconciling the information coming from different clustering methods, are required. An additional requirement for

risk assessment is to determine the efficacy of using clustering methods to refine the projection of the potential for establishment of high risk species by combining regional assemblages with regional climate and habitat variables. Moreover, additional research is needed to investigate whether, in addition to pests and pathogens, the inclusion in the analysis of other associated organisms, such natural enemies, biological control agents, and fungal endophytes, can give stronger and more informative aggregations. Additionally, the analyses presented here are based on political regions where an alternative is to use eco-climatic regions that might provide closer links of the pest profiles with specific host and climate combinations.

Acknowledgements

We thank CABI for making its valuable database freely available for research purposes. This research has received funding from the Bio-Protection Research Centre, Lincoln University, New Zealand, the Co-operative Research Centre for National Plant Biosecurity, Australia, the OECD Co-operative Research Programme, the European Union Seventh Framework Programme FP7 2007–2013 (KBBE 2009-3) under grant agreement 245268 ISEFOR and by a grant from the Swiss State Secretariat for Education and Research to join the COST action ‘PERMIT’.

References

- Abad P, Gouzy J, Aury JM, Castagnone-Sereno P, Danchin EGJ, Deleury E, Perfus-Barbeoch L, Anthouard V, Artiguenave F, Blok VC, Caillaud MC, Coutinho P M, Dasilva C, De Luca F, Deau F, Esquibet M, Flutre T, Goldstone JV, Hamamouch N, Hewezi T, Jaillon O, Jubin C, Leonetti P, Magliano M, Maier TR, Markov GV, McVeigh P, Pesole G, Poulain J, Robinson-Rechavi M, Sallet E, Segurens B, Steinbach D, Tytgat T, Ugarte E, van Ghelder C, Veronico P, Baum TJ, Blaxter M, Bleve-Zacheo T, Davis EL, Ewbank JJ, Favory B, Grenier E, Henrissat B, Jones JT, Laudet V, Maule AG, Quesneville H, Rosso MN, Schiex T, Smant G, Weissenbach J, Wincker P (2008) Genome sequence of the metazoan plant-parasitic nematode *Meloidogyne incognita*. *Nature Biotechnology* 26: 909–915.
- Borgatti SP (1994) How to explain hierarchical clustering. *Connections* 17: 78–80.
- CABI (2003) Crop Protection Compendium, Global Module, 5th edn. CAB International, Wallingford, UK.
- CABI (2007) Crop Protection Compendium, Global Module, 5th edn. CAB International, Wallingford, UK.
- Chon T-S (2011) Self-organising maps applied to ecological sciences. *Ecological Informatics* 6: 50–61.
- Davies DL, Bouldin DW (1979) A cluster separation measure. *IEEE Transactions on Pattern Analysis and Machine Intelligence* 1: 224–227.

- Eschen R, Kenis M (2012) The risk of invasion of Europe by forest pests and diseases, based on their worldwide occurrence. 3rd Meeting of IUFRO Working Unit, June 10-16, Tokyo, Japan. http://hyoka.nenv.k.u-tokyo.ac.jp/alien_reports.html
- Gevrey M, Worner SP, Kasabov N, Giraudeau J-L (2006) Estimating risk of events using SOM models: A case study on invasive species establishment. Ecological Modelling 197: 361–372.
- Gregory FJ, Copestake P, Pearce JM (2007) Key issues in petroleum geology. The Geological Society Publishing House, Bath UK.
- Hansen P, Jaumard B (1997) Cluster analysis and mathematical programming. Mathematical Programming 79: 191–215.
- Hastie T, Tibshirani R, Friedman J (2009) The elements of statistical learning, second edition. Springer, Berlin.
- Heiri O, Lotter AF (2005) Holocene and late glacial summer temperature reconstruction in the Swiss Alps based on fossil assemblages of aquatic organisms: a review. Boreas 34: 506–516.
- Hodda M (2009) Costs of nematodes to Agriculture. Australasian Nematologists Newsletter 9: 15–20.
- Kohonen T (1982) Self-organized formation of topologically correct feature maps. Biological Cybernetics 43: 59–69.
- Kohonen T (2001) Self-Organizing Maps. Springer, Berlin.
- Lek S, Guégan J-F (2000) Artificial neuronal networks. Springer-Verlag, New York.
- Paini DR, Worner SP, Thomas MB, Cook DC (2010a) Using a self organising map to predict invasive species: sensitivity to data errors and a comparison with expert opinion. Journal of Applied Ecology 47: 290–298.
- Paini D, Worner S, Cook D, De Barro P, Thomas M (2010b) Threat of invasive pests from within national borders. Nature Communications 1: 115. doi: 10.1038/ncomms1118
- Paini DR, Bianchi FJJA, Northfield TD, De Barro PJ (2011) Predicting invasive fungal pathogens using invasive pest assemblages: testing model predictions in a virtual world. PLoS ONE 6: e25695.
- Peacock I, Worner SP (2008) Biological and ecological traits that assist establishment of alien invasive insects. New Zealand Plant Protection 61: 1–7.
- Philibert A, Desprez-Loustau M-L, Fabre B, Frey P, Halkett F, Husson C, Lung-Escarmant B, Marçais B, Robin C, Vacher C, Makowski D (2011) Predicting invasion success of forest pathogenic fungi from species traits. Journal of Applied Ecology, 2011, 48: 1381–1390.
- Schmidt A, Law BE, Hanson C, Klemm O (2012) Distinct global patterns of strong positive and negative shifts of seasons over the last 6 decades. Atmospheric and Climate Sciences, 2012, 1: 76–88. doi: 10.4236/acs.2012.21009
- Simberloff D (1989) Which insect introductions succeed and which fail. In: Drake et al. (Eds) Biological Invasions: a global perspective. John Wiley & Sons, New York.
- Singh S, Hodda M, Ash G (2012) A combined approach for better estimation of a species biosecurity risk. Co-operative Centre for National Plant Biosecurity Science Exchange, May, Perth, Australia, 23–25. <http://www.pbcrc.com.au/resource/983>

- Skurka Darin GM, Schoenig S, Barney JN, Dane Panetta F, DiTomaso JM (2011) WHIPPET: A novel tool for prioritizing invasive plant populations for regional Eradication. *Journal of Environmental Management* 92: 131–139.
- Suiter K (2011) Progress on SOM Analysis: A comparison of pre-emergent invasive pests lists using distribution data obtained from the GPDD and CABI databases. *International Pest Risk Mapping and Modelling Workshop V*, 16–18 August, Fort Collins, USA. http://www.pestrisk.org/IPRMW5_Presentations.html
- Vänninen I, Worner S, Huusela-Veistola E, Tuovinen T, Nissinen A, Saikkonen K (2011) Recorded and potential alien invertebrate pests in Finnish agriculture and horticulture. *Agricultural and Food Science* 20: 96–114.
- Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M, Westbrooks R (1997) Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology* 21: 1–16.
- Ward JH Jr. (1963) Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* 48: 236–244.
- Watts MJ, Worner SP (2009a) Predicting the distribution of fungal crop diseases from abiotic and biotic factors using multi-layer perceptrons. *Lecture Notes in Computer Science* 5506: 899–906.
- Watts MJ, Worner SP (2009b) Estimating the risk of insect species invasion: Kohonen self-organising maps versus k-means clustering. *Ecological Modelling* 220: 821–829.
- Watts MJ, Worner SP (2011) Improving cluster-based methods for investigating potential for insect pest species establishment: region-specific risk factors. *Computational Ecology and Software* 1: 138–145.
- Watts MJ, Worner SP (2012) Using artificial neural networks to predict the distribution of bacterial crop diseases from biotic and abiotic factors. *Computational Ecology and software* 2: 70–79.
- Worner SP, Soquet A (2010) A retrospective analysis of the use of ecological theory and pest species assemblages to prioritise pests. 4th International Pest Risk Modelling and Mapping workshop: Pest risk in a changing world. 23–25 August 2010, Port Douglas, Australia. <http://www.pestrisk.org/Workshop2010Report.pdf>
- Worner SP, Gevrey M (2006) Modelling global insect species assemblages to determine risk of invasion. *Journal of Applied Ecology* 43: 858–867.

Understanding trade pathways to target biosecurity surveillance

Manuel Colunga-Garcia¹, Robert A. Haack²,
Roger D. Magarey³, Daniel M. Borchert⁴

1 Center for Global Change and Earth Observations, Michigan State University, 1405 S. Harrison Road, Suite 205, East Lansing, MI 48823 USA **2** USDA Forest Service, Northern Research Station, 1407 S. Harrison Road, Suite 220, East Lansing, MI 48823 USA **3** Center for Integrated Pest Management, North Carolina State University, 1730 Varsity Drive, Suite 300, Raleigh, NC 27606 USA **4** Animal and Plant Health Inspection Service, Plant Protection and Quarantine, Center for Plant Health Science and Technology, Plant Epidemiology and Risk Analysis Laboratory, 1730 Varsity Drive, Suite 300, Raleigh, NC 27606 USA

Corresponding author: Manuel Colunga-Garcia (colunga@msu.edu)

Academic editor: R. Venette | Received 21 September 2012 | Accepted 30 April 2013 | Published 13 September 2013

Citation: Colunga-Garcia M, Haack RA, Magarey RD, Borchert DM (2013) Understanding trade pathways to target biosecurity surveillance. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 103–118. doi: [10.3897/neobiota.18.4019](https://doi.org/10.3897/neobiota.18.4019)

Abstract

Increasing trends in global trade make it extremely difficult to prevent the entry of all potential invasive species (IS). Establishing early detection strategies thus becomes an important part of the continuum used to reduce the introduction of invasive species. One part necessary to ensure the success of these strategies is the determination of priority survey areas based on invasion pressure. We used a pathway-centred conceptual model of pest invasion to address these questions: what role does global trade play in invasion pressure of plant ecosystems and how could an understanding of this role be used to enhance early detection strategies? We concluded that the relative level of invasion pressure for destination ecosystems can be influenced by the intensity of pathway usage (import volume and frequency), the number and type of pathways with a similar destination, and the number of different ecological regions that serve as the source for imports to the same destination. As these factors increase, pressure typically intensifies because of increasing a) propagule pressure, b) likelihood of transporting pests with higher intrinsic invasion potential, and c) likelihood of transporting pests into ecosystems with higher invasibility. We used maritime containerized imports of live plants into the contiguous U.S. as a case study to illustrate the practical implications of the model to determine hotspot areas of relative invasion pressure for agricultural and forest ecosystems (two ecosystems with high potential invasibility). Our results illustrated the importance of how a pathway-centred model could be used to highlight potential target areas for early detection strategies for IS. Many of the hotspots in agricultural and forest ecosystems were within major U.S. metropolitan areas. Invasion ecologists can utilize pathway-centred conceptual models to a) better understand the role of human-mediated pathways in pest establishment, b) enhance current methodologies for IS risk analysis, and c) develop strategies for IS early detection-rapid response programs.

Keywords

Global trade, invasive species, pest risk analysis, early detection, invasion pressure, ecosystem invasibility, propagule pressure, agricultural ecosystems, forest ecosystems

Introduction

Biological invasions can produce severe environmental and economic impacts in plant ecosystems worldwide (Pimentel 2009, Vilà et al. 2010, Scalera 2010, Aukema et al. 2011), and the threat of new invasions will continue to be of global concern in the years ahead (Pejchar and Mooney 2009, Ziska et al. 2010, Lugo and Gonzalez 2010, Pyšek and Richardson 2010, Bradley et al. 2012). Global trade has been widely acknowledged as one of the leading causes of the introduction of invasive species (IS) (Meyer-son and Mooney 2007, Westphal et al. 2008, Hulme 2009, Perrings et al. 2009). In the continuum of approaches used against IS in plant ecosystems, initial efforts are focused on the prevention of their entrance, which is the primary responsibility of the National Plant Protection Organizations (NPPOs) in each country (Magarey et al. 2009). NPPOs, however, face an ever-increasing challenge in this regard. In 1995, the World Trade Organization Agreement on the Application of Sanitary and Phytosanitary Measures (SPS) (SPS Agreement) entered into force. With regard to plant ecosystems, the SPS Agreement lays out rights and obligations for member countries to protect the health of plants from the introduction and spread of pests and diseases. The SPS Agreement requires measures, commonly based on international standards, which are aimed to prevent the entry of pests and diseases while ensuring that such measures are not used as unjustified barriers to trade. SPS measures that are not based on international standards must be technically justified and based on scientific evidence (usually through a risk assessment) (World Trade Organization 2010). Despite SPS measures and related efforts by countries to prevent the entry of IS there is the potential of novel introductions with increasing trends in the volume and origin of international cargo. This underscores the importance of establishing early-detection strategies for the detection of IS that may be introduced into a country.

Given the above challenges, countries implement approaches against IS based on early detection-rapid response strategies (Mehta et al. 2007, Rabaglia et al. 2008, Simpson et al. 2009, Britton et al. 2010). These strategies include the following components: a) detection networks including syndromic surveillance; b) research and training; c) stakeholder participation; d) integration of technologies to facilitate detection and communication of knowledge, skills, and data; and e) taxonomic support, including availability of voucher specimens and authoritative verifications (National Invasive Species Council 2003). Early detection networks, often operating under limited resources, should focus on high-priority targets including “high-risk locations, high-value resources, important pathways, and populations and species of specific concern” (National Invasive Species Council 2003). For the particular case of trade-mediated introductions, we propose in this paper to include the concept of invasion pressure as a criterion to highlight poten-

tial at-risk locations for early detection purposes. Invasion pressure, which is the probability that an ecosystem experiences an invasion within a specified time period, results from the interaction of three factors: propagule pressure, species invasion potential, and ecosystem invasibility (Lonsdale 1999, Davis 2009). For the purpose of this paper, we define propagule as a shipment in a pathway at any point in time and space that is infested, infected, or contaminated by IS. We assume that IS are viable at arrival and have an intrinsic potential to establish. Building on the definition of the International Plant Protection Convention (2012a), a pathway is any means (commodity, container, and/or conveyance) that allows the entry or spread of IS. Propagule pressure is thus a measure of the number of individuals in a shipment and the rate at which shipments arrive per unit of time (Simberloff 2009). Species invasion potential is the intrinsic ability of species to invade an ecosystem (di Castri 1989). Finally, ecosystem invasibility is the overall susceptibility of an ecosystem (Williamson 1996) due to factors such as climate, susceptibility of native species, and disturbance. To use the invasion pressure criterion in the selection of target locations for early detection programs, we need to answer two questions: what role does global trade play in invasion pressure of plant ecosystems, and how could an understanding of this role be used to enhance early detection strategies?

To answer the above questions, we framed the interaction between global trade and biological invasions using a pathway-centred invasion model (Fig. 1). As previously defined, a pathway can be any combination of a commodity, a container, or a conveyance (truck, plane, marine vessel, etc.) that facilitates the entry of an IS. It implies the existence of an origin and a destination, which in our model we label as the source and destination ecosystems, respectively. The uptake phase occurs when an IS infests (or infects, in the case of pathogens) a commodity, or when an IS is simply present (as a contaminant) on a commodity, or on or in a container or conveyance. The transport phase is the movement of the conveyance from origin to destination. The release phase of IS takes place at the destination end of the pathway and either of two situations can lead to an invasion. First, the IS can be released into a suitable habitat (in which case release and entry occur simultaneously). Second, the IS can be released into a situation that facilitates access to a suitable habitat (in which case release and entry are separated in time). The uptake, transport, and release phases are driven by logistic and freight distribution processes dictated by urban, production, and transportation systems. After release, ecological processes take over to determine whether the IS is able to establish and spread. Ecological processes also influence the occurrence of IS during the uptake phase.

What then is the answer to our first question, i.e., what role does global trade play in invasion pressure of plant ecosystems? Based on the pathway-centred invasion model (Fig. 1), the level of invasion pressure experienced by destination ecosystems can be influenced by the intensity of pathway usage, the number of pathways with similar destinations, and the number of different ecological source regions for imports to the same destination. High-intensity pathway usage, high numbers of single destination pathways, and high numbers of source ecological regions can result in high invasion pressure because they increase a) propagule pressure, b) the diversity of IS transported (which may increase the likelihood of transporting IS with high intrinsic invasion potential),

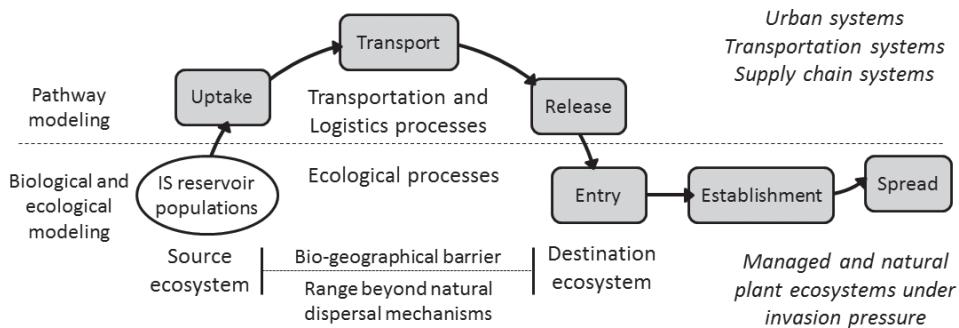


Figure 1. Schematic diagram of a multi-stage invasion model that links global movement of traded goods (as part of the transportation and supply chain systems) to movement of invasive species (IS). This model was adapted from Isard et al. (2005) in which long-range dispersion of invasive species was depicted via atmospheric pathways and also includes concepts by Colautti and MacIsaac (2004) and Rodrigue et al. (2009).

and c) the likelihood of transporting IS that can take advantage of an ecosystem with high potential invasibility. It is important however, to clarify that when propagule pressure is estimated using a proxy variable (e.g., volume of freight shipments) we cannot estimate invasion pressure per se. This is because we do not know the type and number of IS (if any) present in the freight shipment. Instead we should use the term relative invasion pressure to emphasize the fact that high and low values (of invasion pressure) are only relative to the space/time continuum under study. Subsequent risk analysis could be implemented to determine the actual risk experienced by areas under high relative invasion pressure. To answer the second question (how could an understanding of this role be used to enhance early detection strategies?), we will illustrate the use of this model to characterize the relative invasion potential of two plant ecosystems with a case study. In this case study, we will quantify the relative invasion pressure in agricultural and forest ecosystems due to U.S. imports via a single pathway (maritime containerized imports of live plants). Foreshadowing our results, we will show that this pathway places higher relative invasion pressure on several agricultural and forest areas in the U.S., including many that occur within major metropolitan areas. Finally, we will highlight the implications of our model for researchers and policymakers who deal with IS. We anticipate that the principles discussed in the present paper can also be applied and utilized as a framework to examine the invasion pressure of plant ecosystems via other pathways.

Case study: U.S. maritime containerized imports of live plants

Background

The value of global live plant trade has increased worldwide in the last decade (Fig. A1 in Appendix). Globally in 2011, the U.S. ranked 9th in exports and 2nd in imports

with 2% and 9.3% shares of the world exports and imports of live plants, respectively (Tables A1, A2 in Appendix). Maritime containerized imports represented 64.4% of the total value of all live plants imported into the U.S. in 2010. This value is after excluding fresh cut flowers (which are imported almost exclusively via the air conveyance pathway) (Table A3 in Appendix) and live plant imports from Mexico and Canada (which are imported via the land conveyance pathway such as truck or rail) (Table A4 in Appendix). The increase in trade of live plants has intensified concerns as they constitute a pathway for the introduction of invasive plant pests or pathogens (Reichard and White 2001, Brasier 2008, Drew et al. 2010, Bradley et al. 2012, Liebhold et al. 2012, Parke and Grünwald 2012). In fact, on a commodity categorization scale of 1 to 4 where 4 represents commodities with the highest potential to introduce and spread pests, live plants are categorized as either 3 or 4 (International Plant Protection Convention 2009). Category 3, which includes cut flowers, refers to commodities that have not been processed and are intended for consumption or processing. Category 4 includes commodities that have not been processed and whose intended use is planting. Live plants in this last category (serially ranked from highest to lowest based on risk) include rooted plants in pots; bare root plants; bulbs and tubers; root fragments, root cuttings, rootlets or rhizomes; rooted cuttings; unrooted cuttings; and budwood/graftwood (International Plant Protection Convention 2012b). U.S. regulations of live plant imports are implemented via Plant Inspection Stations which besides inspections make sure that standard protocols for treatments are followed (Animal and Plant Health Inspection Service 2007, 2011, 2012a,b). When high risk IS are found associated with the imported live plants, fumigation treatments are implemented, a procedure that often targets other IS present on the commodity.

Methods

To quantify the intensity of pathway usage we acquired a full set of PIERS[®] (<http://www.piers.com>) records for U.S. maritime containerized imports of live plants (Harmonized System Code = 06) during 2010. Data fields included vessel name, number of TEUs (i.e., Twenty-Foot Equivalent Unit containers), tonnes, place/port of container loading with live plants, and U.S. port of destination. Places/ports were geocoded using a variety of public domain sources including the World Port Source[®], GEOnet Names Server (GNS), and Bing[®] maps. In the case of places whose names were the same as other places in the same country, an effort was made to search online to determine if those names were associated with places that commonly exported live plants. If this was not successful, the place was not included in the analysis. Because some U.S. ports that are involved in live plant trade are in close geographic proximity to each other (e.g., the ports of Long Beach and Los Angeles in California), we grouped them by their encompassing metropolitan area. Finally, we computed the daily number of TEUs between the origin of the containers (i.e., the place/port where live plants were loaded into a container) and the destination (i.e., the U.S. metropolitan area of the

port of entry). Because data records in PIERS[®] include fractions of TEUs (i.e., when only a portion of a container is occupied with live plants), the sum of TEUs becomes only a measure of import volume and does not reflect the actual number of individual containers. Due to data availability for this study, our analysis focused on live plants in general. However, Tables A3 and A4 in Appendix provide insight into the types of live plants that were included in the maritime containerized imports to the U.S. in 2010 (and hence in the analyses found in this paper).

To provide an indicator of the potential diversity of IS transported into the U.S. we quantified the number of ecological regions from which live plant imports originated throughout the world and where they entered and moved to in the U.S., we used the world ecoregion classification by Olson et al. (2001). This classification system divides the world into 14 biomes, which are subdivided into 867 ecoregions. Each port or place of origin for the live plant imports in our dataset was assigned to the biome and ecoregion it intersected. We computed the number of biomes and associated ecoregions that served as the origin for the live plant imports that arrived in each U.S. metropolitan area and state.

To determine areas beyond the U.S. ports of entry that could be under high relative invasion pressure we modelled the final destination of live plant imports at the U.S. county level. First we acquired monthly data on U.S. maritime containerized imports of live plants during 2010 from USA Trade[®] Online (<https://www.usatrade-online.gov>). This dataset included country of origin, weight imported, and U.S. state of destination. Then we acquired from Hoovers Inc. (<http://www.hoovers.com>) a list of geocoded retail nurseries, garden stores and other establishments engaging in the sale of ornamental nursery products in 2010–2011. This list contained, among other information, the total revenue per establishment, which was used to obtain the total revenue for all establishments within a county. We aggregated the revenue at the county level due to the uncertainty of knowing which establishments actually imported live plants in 2010. Moreover, sales of live plants are not occurring only at those specialized establishments, but also at home improvement stores and mass merchandisers throughout the U.S. (Waterman 2012). Therefore, revenue was used as an indicator of live plant demand in a county. We then computed the proportion of county revenue with respect to the total state revenue. This proportion was used as a weight factor to disaggregate State imports of live plants and produce a map of the likely destinations of live plant imports at the county level. This county-level map was intersected with the county centroids of the U.S. land-use based maps (agriculture and forest) from Colunga-Garcia et al. (2010a). Using the resulting maps (agriculture and forest centred maps for counties that were destinations for live plant imports) we estimated hotspots for potential invasion in those two plant ecosystems. To perform this procedure we used the software GeoDa (Anselin et al. 2006) and computed the Moran's I to detect clusters of counties with high volume of imports. Moran's I is a local indicator of spatial association (Anselin 1995), and in our case, it detected which counties were the destinations of significantly higher volume of live plant imports than the mean volume for the entire contiguous U.S. (Fortin and Dale 2005).

Results

Live plant imports to the U.S. in 2010 that entered via the maritime containerized pathway originated from 276 distinct places in 76 countries. These imports arrived at U.S. seaports located in 15 metropolitan areas within 13 states of the contiguous U.S. (Fig. 4B). Three metropolitan areas accounted for 72.2% of all containerized live-plant maritime imports entering the U.S. in 2010: Los Angeles-Long Beach-Santa Ana in the state of California (37.3%), New York-Northern New Jersey-Long Island which included parts of the states of New York, New Jersey, and Pennsylvania (23.3%); and Miami-Fort Lauderdale-Pompano Beach in the state of Florida (11.6%) (Fig. 2). For brevity we designated those metropolitan areas as Los Angeles, New York, and Miami, respectively. The source areas of these live plant imports represented 102 ecoregions within 13 biomes (Fig. 4A). However, 40.4% of the live plant imports originated from the temperate broadleaf/mixed forest and 40% came from the tropical and subtropical moist broadleaf forest biome. In addition, the source areas within these same two biomes contributed 53% of the 102 ecoregions, representing 31 and 23 ecoregions, respectively. The three aforementioned metropolitan areas not only received large volumes of live plant imports but also received imports from a large number of ecoregions (Fig. 2). A visual display of the variation in weekly imports of live plants in 2010 by

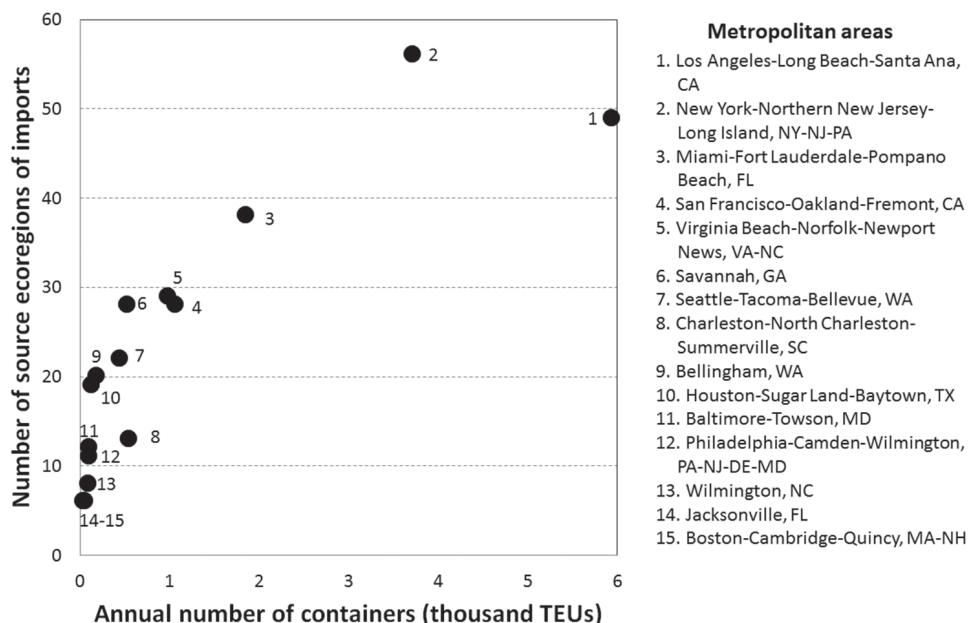


Figure 2. Relative invasion pressure of invasive species (IS) at seaports within selected metropolitan areas in the contiguous U.S. via maritime containerized imports of live plants. The number of source ecoregions is used as an indicator of potential IS diversity, while the number of containers (TEU = container length in Twenty-foot Equivalent Units) with live plants is used as an indicator of relative IS propagule pressure. Data sources: PIERs® port to port data and World Ecoregions (Olsen et al. 2011).

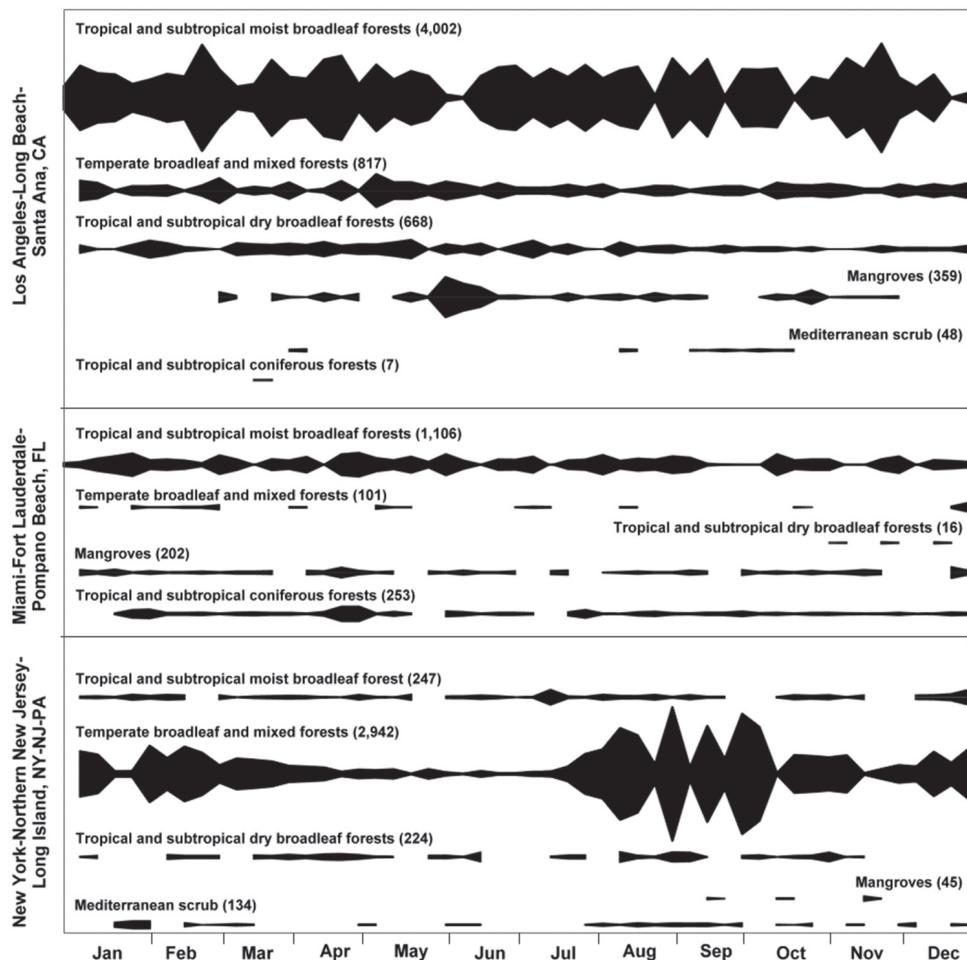


Figure 3. Trend in weekly number of maritime containerized imports (TEUs) of live plants entering the contiguous U.S. in 2010 at seaports in three selected metropolitan areas. Imports were classified according to the likely biome where the live plants were loaded within the country of origin. Numbers in parentheses for each biome refer to the total number of containers (TEUs) that arrived with live plants in 2010. The blackened areas for each biome type represent the trend in live plant imports at weekly intervals in 2010 based on the total number of TEUs indicated in parenthesis. PIERS® port to port data and World Ecoregions (Olsen et al. 2011).

biome of the source area (Fig. 3) showed that the New York metropolitan area exhibited certain seasonality in imports with a large spike between the months of August and October and less activity between May and June. In contrast, the other two metropolitan areas depicted in Fig. 3 (Los Angeles and Miami) showed less variation in the volume of imports throughout the year. Another observation to note is that while the tropical and subtropical moist broadleaf forests biome was a major contributor to the live plant imports entering Los Angeles and Miami, the temperate broadleaf/mixed forest biome was the major contributor for imports entering New York.

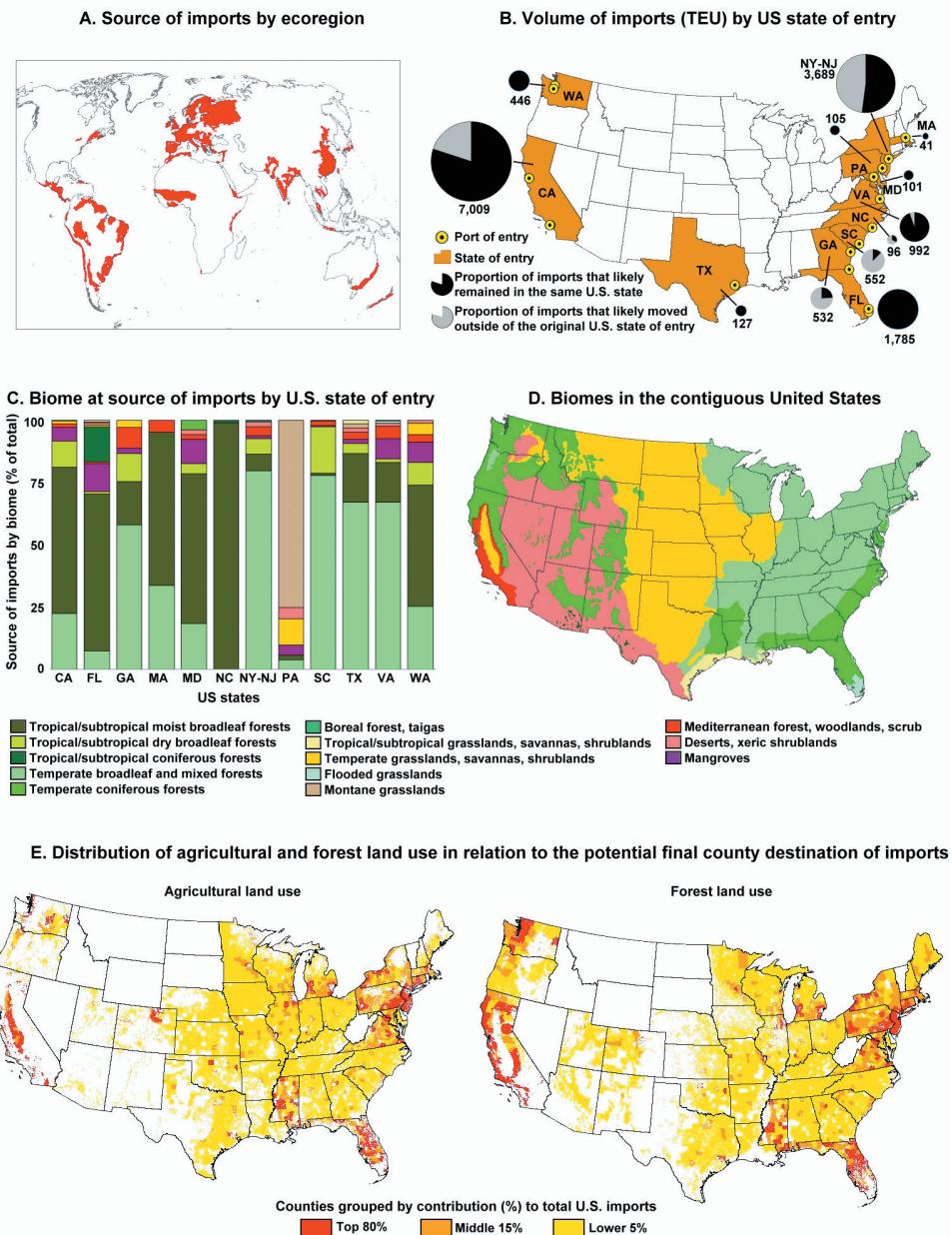


Figure 4. Maritime containerized imports of live plants entering the contiguous U.S. in 2010 from their source to their final destination. **A** Likely source areas of imported live plants by ecoregions (areas in red) **B** Volume of imports (TEUs) with live plants by U.S. state of entry. State abbreviations: CA California, FL Florida, GA Georgia, MA Massachusetts, MD Maryland, NC North Carolina, NY-NJ New York-New Jersey, PA Pennsylvania, SC South Carolina, TX Texas, VA Virginia, WA Washington **C** Biome at the source of the imported live plants by destination state **D** Biomes of the contiguous U.S. **E** Distribution of agricultural and forest land use in relation to the potential final county destination of live plant imports.

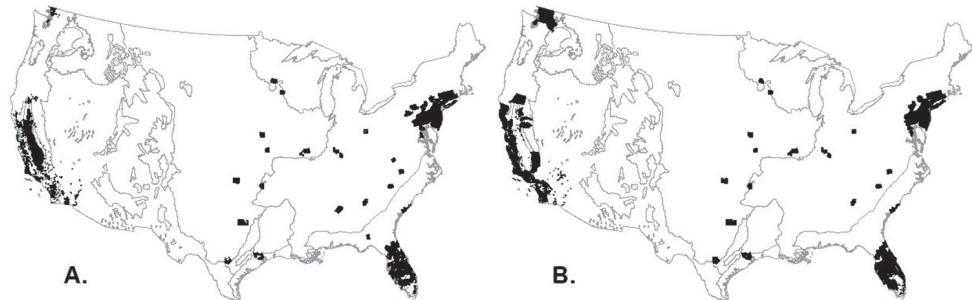


Figure 5. Potential hotspots of relative invasion pressure to IS associated with maritime containerized imports of live plants in the contiguous U.S. in 2010. **A** Agricultural ecosystems **B** Forest ecosystems. Contour lines separate major U.S. biomes as shown in Fig. 4E.

The maps in Fig. 4E indicate that many counties (2,422) served as the likely final destination for the live plant imports that arrived in the U.S. via the maritime containerized pathway in 2010. Overall, the top 80% of live plant imports (by volume) were likely shipped to 182 counties in the contiguous U.S., the next 15% of the imports went to another 368 counties, and the remaining 5% of imports went to another 1872 counties (Tables A5, A6 in Appendix). Of the 182 counties that received 80% of the imports in 2010, 154 (84.6%) were located in metropolitan areas and received 74.2% of all live plant imports that entered the contiguous U.S. The analysis (Fig. 5) revealed that most of California, Florida, New Jersey, and Connecticut and portions of Washington, New York, Pennsylvania, and Maryland are potentially under high relative invasion pressure under the analyzed pathway. Of the 157 U.S. counties that fell within hotspots of relative invasion pressure, 154 had agricultural land and 143 had forest land, and of these, 134 (87%) and 125 (87.4%) counties, respectively, fell within metropolitan areas. The counties with agricultural and forest ecosystems received 64.5 and 63.3% of the live plant imports to the contiguous U.S. in 2010, respectively.

Discussion

At the beginning of this paper, we posed two questions: What role does global trade play in invasion pressure of plant ecosystems? And how could an understanding of this role be utilized to enhance early detection strategies? We answered the first question in the introduction by explaining the implications of a pathway centred invasion model. We addressed the second question with the case study. Given the risk of live plant imports as an IS pathway (International Plant Protection Convention 2009), USDA-APHIS puts special effort in the surveillance of this pathway (Animal and Plant Health Inspection Service 2007). However, IS that escape detection at ports of entry could potentially establish in the hotspot areas of relative invasion pressure identified by our model. The hotspot areas in the northeastern U.S. (Fig. 5) are likely the result of imports entering the

New York metropolitan area, which is a major gateway for large volumes of imports that originate from many different world ecoregions (Fig. 2). The major biome encompassing the hotspots in the northeastern U.S. (i.e., temperate broadleaf/mixed forest) (compare Figs. 4D and 5) is similar to the dominant biome that is the source of most live-plant imports that enter through the New York metropolitan area (Fig. 3). Such a relationship between source and destination biomes indicates that IS that gain access to plant ecosystems in the northeastern hotspot areas are likely to find suitable conditions for their establishment. In contrast with the northeastern hotspots, a mixture of biomes comprises the source regions for live plant imports in the southwestern U.S. and these do not match well with the biomes that encompass the hotspots. This does not preclude invasion in the Southwest, but it forces one to think about what types of IS would thrive best in such hotspots and under what circumstances. The use of irrigation or other manipulations of the environment in the Southwest may provide suitable microclimates for IS to establish. If these areas are recognized as being within a hotspot for relative invasion pressure and a subsequent risk analysis determines the area as high risk then by regularly monitoring for IS there is a good chance that new IS will be detected relatively soon after establishment.

An important insight for early detection strategies is that the majority of U.S. counties experiencing high relative invasion pressure (Fig 4E, 5) are located in metropolitan areas. In assessing the implications of this, it is necessary to realize that the term “metropolitan” is not synonymous with “urban” (at least in the U.S.) (Office of Information and Regulatory Affairs 2010). In U.S. metropolitan areas only 11% of the area is classified as developed land. Other land uses, such as forest, agriculture, and shrub/scrub account collectively for 70% of the land in metropolitan areas (Table A7 in Appendix). One key characteristic of metropolitan areas—the economic interactions between urban and rural areas—makes them a fertile ground for the establishment and spread of IS. Consequently, plant ecosystems within metropolitan areas that include hotspots are also under high relative invasion pressure.

From a research perspective there is a strong need to characterize in more detail the IS propagule pressure entering a country, i.e., what life stages are commonly associated with the uptake and transportation processes? Such an analysis could be conducted by combining a) high-resolution trade data (e.g., port to port), b) models developed to determine the location and extent of foreign regions that could potentially serve as the source of IS, and c) models for the growth and dispersion of IS around foreign logistic-network facilities (e.g., port terminals). The results of such analyses could then be applied at the release stage of the invasion model to determine the interacting mechanisms between IS biological traits and propagules that allow them to reach suitable habitats. In addition, further refinements are needed in the approach we used in our case study. For instance, we assumed that the origin of the imported live plants was near the place where the live plants were loaded into the containers (from a logistics perspective that assumption may make sense). However, implementing a probabilistic gravity model could account for the potential that other nearby ecological regions could be the source of the imports. Also, we assumed in our approach that IS potentially associated with live plants were due to infestations that occurred in the country of origin. However, we recognize that plants could be-

come infested throughout the entire trade network, including when a container is opened at each port visited until the final destination is reached (Kaluza et al. 2010, Keller et al. 2010, Paini and Yemshanov 2012). Similarly, for the final destination of the imported live plants, we used information related to commercial business establishments in the U.S. that are involved in the sale of ornamental/nursery plants. However, as these relatively small commercial establishments keep losing market share to mass merchandisers and large home improvement stores, there will be a need to adjust our analytical approach.

From a policy perspective, there is a need to further develop strategies that more effectively acquire and incorporate trade information in pest risk analysis. We showed in our case study the importance of information such as daily port-to-port import data from all countries of the world to the United States that included the type of imported commodities. Such information may already exist (Sparka 2010) and it may already be available as a commercial database for selected countries (e.g., Piers® in our case study). Similarly, there is interest in developing early detection strategies that can help improve the decision processes regarding which IS to select for monitoring efforts. One way to improve the process would be to change the focus from individual pest species of concern to geographic areas or regions of concern. As stated above, areas with ecosystems under higher invasion pressure are likely to continue to be under higher invasion pressure in the future. Focusing surveillance efforts in such high-risk areas should increase the likelihood of early detection of IS (Colunga-Garcia et al. 2010b).

For the past few years the invasion literature has repeatedly noted the importance of global trade. Invasion ecologists can utilize a pathway centred conceptual model as described in the present paper as a framework to a) better understand the role of human-mediated pathways, b) enhance current methodologies for pest risk analysis, and c) develop strategies for IS early detection-rapid response programs.

Acknowledgements

We thank Eva Kassens-Noor, Janice Molloy, Trixie Smith, Wen Li, Robert Venette, and two anonymous reviewers for providing comments to enhance this manuscript. This project was made possible, in part, by a Cooperative Agreement from the United States Department of Agriculture's Animal and Plant Health Inspection Service (APHIS) to the first author. The information and views set out in this paper are those of the authors and it may not necessarily express USDA-APHIS views.

References

- Animal and Plant Health Protection Service (2007) Plant Inspection Station strategic plan 2007–2012. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine, Washington, D.C., 1–24.

- Animal and Plant Health Inspection Service (2011) Bulb Preclearance Program Identification Manual. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine, Washington, D.C., 1–301.
- Animal and Plant Health Inspection Service (2012a) Cut Flowers and Greenery Import Manual. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine, Washington, D.C., 1–156.
- Animal and Plant Health Inspection Service (2012b) Plants for Planting Manual. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine, Washington, D.C., 1–620.
- Anselin L (1995) Local indicators of spatial association - LISA. *Geographical Analysis* 27: 93–115. doi: 10.1111/j.1538-4632.1995.tb00338.x
- Anselin L, Syabri I, Kho Y (2006) GeoDa: An introduction to spatial data analysis. *Geographical Analysis* 38: 5–22. doi: 10.1111/j.0016-7363.2005.00671.x
- Aukema JE, Leung B, Kovacs K, Chivers C, Britton KO, Englin J, Frankel SJ, Haight RG, Holmes TP, Liebhold AM, McCullough DG, Von Holle B (2011) Economic impacts of non-native forest insects in the continental United States. *PLoS ONE* 6: 1–7. e24587. doi: 10.1371/journal.pone.0024587
- Bradley BA, Blumenthal DM, Early R, Grosholz ED, Lawler JJ, Miller LP, Sorte CJB, D'Antonio CM, Diez JM, Dukes JS, Ibanez I, Olden JD (2012) Global change, global trade, and the next wave of plant invasions. *Frontiers in Ecology and the Environment* 10:20–28. doi: 10.1890/110145
- Brasier CM (2008) The biosecurity threat to the UK and global environment from international trade in plants. *Plant Pathology* 57: 792–808. doi: 10.1111/j.1365-3059.2008.01886.x
- Britton KO, White P, Kramer A, Hudler G (2010) A new approach to stopping the spread of invasive insects and pathogens: early detection and rapid response via a global network of sentinel plantings. *New Zealand Journal of Forestry Science* 40: 109–114.
- Colunga-Garcia M, Magarey RA, Haack RA, Gage SH, Qi J (2010a) Enhancing early detection of exotic pests in agricultural and forest ecosystems using an urban-rural gradient framework. *Ecological Applications* 20: 303–310. doi: 10.1890/09-0193.1
- Colunga-Garcia M, Haack RA, Magarey RA, Margosian ML (2010b) Modeling spatial establishment patterns of exotic forest insects in urban areas in relation to tree cover and propagule pressure. *Journal of Economic Entomology* 103: 108–118. doi: 10.1603/EC09203
- Davis MA (2009) Invasion biology. Oxford University Press, New York, 1–244.
- di Castri F (1989) History of biological invasions with special emphasis on the old world. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M (Eds) *Biological invasions: a global perspective*. John Wiley, Chichester, UK, 1–30.
- Drew J, Anderson N, Andow D (2010) Conundrums of a complex vector for invasive species control: a detailed examination of the horticultural industry. *Biological Invasions* 12: 2837–2851. doi: 10.1007/s10530-010-9689-8
- Fortin M, Dale M (2005) Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge, United Kingdom, 1–365.

- Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18. doi: 10.1111/j.1365-2664.2008.01600.x
- International Plant Protection Convention (2009) International standards for phytosanitary measures: ISPM No. 32. Categorization of commodities to their pest risk. Food and Agriculture Organization of the United Nations, Rome, Italy, 1–16.
- International Plant Protection Convention (2012a) International standards for phytosanitary measures: ISPM No. 5. Glossary of phytosanitary terms. Food and Agriculture Organization of the United Nations, Rome, Italy, 1–38.
- International Plant Protection Convention (2012b) International Standards for Phytosanitary Measures: ISPM No. 36. Integrated measures for plants for planting. Food and Agriculture Organization of the United Nations, Rome, Italy, 1–20.
- Kaluza P, Kölzsch A, Gastner MT, Blasius B (2010) The complex network of global cargo ship movements. *Journal of the Royal Society Interface* 7: 1093–1103 doi: 10.1098/rsif.2009.0495
- Keller RP, Drake JM, Drew MB, Lodge DM (2010) Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. *Diversity and Distributions* 17: 93–102. doi: 10.1111/j.1472-4642.2010.00696.x
- Liebhold AM, Brockhoff EG, Garrett LJ, Parke JL, Britton KO (2012) Live plant imports: The major pathway for forest insect and pathogen invasions of the United States. *Frontiers in Ecology and the Environment* 10: 135–143. doi: 10.1890/110198
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80: 1522–1536. doi: 10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO;2
- Lugo AE, Gonzalez G (2010) Changing conditions and changing ecosystems: A long-term regional and transcontinental research approach on invasive species. In: Dix ME, Britton K (Eds) *A dynamic invasive species research vision: opportunities and priorities 2009–29*. Gen. Tech. Rep. WO-79/83. U.S. Department of Agriculture, Forest Service, Research and Development, Washington, D.C., 121–126.
- Magarey RD, Colunga-Garcia M, Fieselmann DA (2009) Plant biosecurity in the United States: roles, responsibilities and information needs. *BioScience* 59: 875–884. doi: 10.1525/bio.2009.59.10.9
- Mehta SV, Haight RG, Homans FR, Polasky S, Venette RC (2007) Optimal detection and control strategies for invasive species management. *Ecological Economics* 61: 237–245. doi: 10.1016/j.ecolecon.2006.10.024
- Meyerson LA, Mooney HA (2007) Invasive alien species in an era of globalization. *Frontiers in Ecology and the Environment* 5: 199–208. doi: 10.1890/1540-9295(2007)5[199:IAS]IAE]2.0.CO;2
- National Invasive Species Council (2003) General guidelines for the establishment and evaluation of invasive species early detection and rapid response systems Version 1. U.S. Department of the Interior, Office of the Secretary, Washington, D.C., 1–16.
- Office of Information and Regulatory Affairs (2010) 2010 standards for delineating metropolitan and micropolitan statistical areas. U.S. Office of Management and Budget. *Federal Register* 75: 123 (28 June 2010), 37246–37252.

- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettenberg WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* 51: 933–938. doi: 10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2
- Paini DR, Yemshanov D (2012) Modelling the arrival of invasive organisms via the international marine shipping network: A Khapra beetle study. *PLoS ONE* 7: 1–9. e44589. doi: 10.1371/journal.pone.0044589
- Parke JL, Grünwald NJ (2012) A systems approach for management of pests and pathogens of nursery crops. *Plant Disease* 96: 1236–1244. doi: 10.1094/PDIS-11-11-0986-FE
- Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. *Trends in Ecology and Evolution* 24: 497–504. doi: 10.1016/j.tree.2011.03.031
- Perrings C, Fenichel E, Kinzig A (2009) Globalization and invasive alien species: trade, pests, and pathogens. In: Perrings C, Mooney H, Williamson M (Eds) *Bioinvasions and Globalization: Ecology, Economics, Management, and Policy*. Oxford University Press, Oxford, 42–55. doi: 10.1093/acprof:oso/9780199560158.003.0004
- Pimentel D (2009) Invasive plants: their role in species extinctions and economic losses to agriculture in the USA. In: Inderjit (Ed) *Management of invasive weeds*. Springer Science + Business Media B.V., Netherlands, 1–7.
- Pyšek P, Richardson DM (2010) Invasive Species, Environmental Change and Management, and Health. *Annual Review of Environment and Resources* 35: 25–55. doi: 10.1146/annurev-environ-033009-095548
- Rabaglia RJ, Duerr D, Acciavatti R, Ragenovich I (2008) Early detection and rapid response for non-native bark and Ambrosia beetles. USDA Forest Service, Forest Health Protection, Washington, D.C., 1–12.
- Reichard SH, White P (2001) Horticulture as a pathway of invasive plant introductions in the United States. *BioScience* 51: 103–113. doi: 10.1641/0006-3568(2001)051[0103:HAAPOI]2.0.CO;2
- Scalera R (2010) How much is Europe spending on invasive alien species? *Biological Invasions* 12: 173–177. doi: 10.1007/s10530-009-9440-5
- Simberloff D (2009) The role of propagule pressure in biological invasion. *Annual Review of Ecology, Evolution, and Systematics* 40: 81–102. doi: 10.1146/annurev.ecolsys.110308.120304
- Simpson A, Jarnevich C, Madsen J, Westbrooks R, Fournier C, Mehrhoff L, Browne M, Graham J, Sellers E (2009) Invasive species information networks: collaboration at multiple scales for prevention, early detection, and rapid response to invasive alien species. *Biodiversity* 10: 5–13. doi: 10.1080/14888386.2009.9712839
- Sparka F (2010) Jurisdiction and arbitration clauses in maritime transport documents: A comparative analysis. Springer-Verlag, Berlin, Heidelberg, 1–281.
- Vilà M, Basnou C, Pysvek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE, DAISIE partners (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* 8: 135–144. doi: 10.1890/080083

- Waterman J (2002) Drying up: Consumers will seek out bargains from mass retailers, hurting traditional nurseries. IBISWorld Industry Report 44422 Nursery & Garden Stores in the US, 1–27.
- Westphal MI, Browne M, MacKinnon K, Noble I (2008) The link between international trade and the global distribution of invasive alien species. *Biological Invasions* 10: 391–398. doi: 10.1007/s10530-007-9138-5
- Williamson M (1996) Biological invasions. Chapman and Hall, London, UK, 1–244.
- World Trade Organization (2010) The WTO Agreements Series Sanitary and Phytosanitary Measures. World Trade Organization, Switzerland, 1–45.
- Ziska LH, Blumenthal DM, Runion GB, Hunt Jr ER, Diaz-Soltero H (2010) Invasive species and climate change: an agronomic perspective. *Climatic Change* 105: 13–42. doi: 10.1007/s10584-010-9879-5

Appendix

Global trade and invasion pressure in plant ecosystems: Supplementary figures and tables. (doi: 10.3897/neobiota.18.4019.app1) File format: Acrobat Adobe document (pdf).

Explanation note: Worldwide annual value (USD) for four categories of live plant imports from 2001–2011 (Fig. A1). Top 10 world exporting (Table A1) and importing (Table A2) countries of live plants in 2011. Value of U.S. live plant imports from all world regions except NAFTA (Mexico and Canada) (Table A3) and from the NAFTA region only (Table A4). Characterization of U.S. counties with agricultural (Table A5) and forest (Table A6) land use that were a potential destination of maritime containerized imports of live plants in 2010. Percentage of land use/cover types in the metropolitan areas of the U.S. (Table A7).

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Citation: Colunga-Garcia M, Haack RA, Magarey RD, Borchert DM (2013) Understanding trade pathways to target biosecurity surveillance. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. *NeoBiota* 18: 103–118. doi: 10.3897/neobiota.18.4019 Global trade and invasion pressure in plant ecosystems: Supplementary figures and tables. doi: 10.3897/neobiota.18.4019.app1

Improving pest risk assessment and management through the aid of geospatial information technology standards

Trond Rafoss¹, Jarle Skahjem², John Atle Johansen², Ståle Johannessen², Udaya Sekhar Nagothu¹, Inger S. Fløistad¹, Arild Sletten¹

1 Bioforsk – Norwegian Institute for Environmental and Agricultural Research, Høgskoleveien 7, 1342 Ås, Norway **2** Geoport AS, Kongens gate 33, 4608 Kristiansand, Norway

Corresponding author: Trond Rafoss (trond.rafoss@bioforsk.no)

Academic editor: Rob Venette | Received 26 September 2012 | Accepted 29 July 2013 | Published 13 September 2013

Citation: Rafoss T, Skahjem J, Johansen JA, Johannessen S, Nagothu US, Fløistad IS, Sletten A (2013) Improving pest risk assessment and management through the aid of geospatial information technology standards. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 119–130. doi: [10.3897/neobiota.18.4017](https://doi.org/10.3897/neobiota.18.4017)

Abstract

Delivery of geospatial information over the Internet for the management of risks from invasive alien species is an increasingly important service. The evolution of information technology standards for geospatial data is a key factor to simplify network publishing and exchange of maps and data. The World Wide Web Consortium (W3C)-geolocation specification is a recent addition that may prove useful for pest risk management. In this article we implement the W3C-geolocation specification and Open Geospatial Consortium (OGC) mapping standards in a Web browser application for smartphones and tablet computers to improve field surveys for alien invasive species. We report our first season field experiences using this tool for online mapping of plant disease outbreaks and host plant occurrence. It is expected that the improved field data collection tools will result in increased data availability and thereby new opportunities for risk assessment, because data-needs and availability are crucial for species distribution modelling and model-based forecasts of pest establishment potential. Finally, we close with a comment on the future potential of geospatial information standards to enhance the translation from data to decisions regarding pest risks, which should enable earlier detection of emerging risks as well as more robust projections of pest risks in novel areas. The forthcoming standard for processing of geospatial information, the Web Processing Standard (WPS), should open new technological capabilities both for automatic initiation and updating of risk assessment models based on new incoming data, and subsequent early warning.

Keywords

Pest, risk, mapping, mobile, GPS, geospatial, standards

Introduction

Historical evidence shows that species composition and abundance are changing in time and space. This is not only evident in natural ecosystems, but also in managed ecosystems like agriculture and forestry. However, the rate of change has increased dramatically in modern times due to the globalization of trade and the movement of organisms to parts of the world where they have not been before. Climate change is expected to further affect species' distributions and their phenology. The risks related to these changes are well known for both natural and agricultural resources, including loss of biodiversity, crop loss and increased pest problems (Mooney and Hobbs 2000).

When human society faces major new global challenges, solutions based on new technological developments are commonly suggested. So what about technological solutions for reducing pest risks? The role of technology for reducing these risks has received some attention in the literature. Baker et al. (2005) discussed novel strategies for the future management of the risks posed by invasive species to global crop production and biodiversity. They mentioned new mobile computing, Global Positioning System (GPS), digital photography and telephone technologies as potential tools that could greatly enhance the management of pest outbreaks by facilitating rapid transmission of key data between the field, lab and senior staff overseeing operations. They also mentioned Geographical Information Systems (GIS) for mapping and forecasting as invaluable to formulate contingency plans, containment strategies, and eradication campaigns against pests. For pest risk management of fire blight caused by the plant pathogenic bacterium *Erwinia amylovora*, Rafoss et al. (2010) demonstrated how the use of a generic application integrating mobile computing and mapping with GPS on a simple mobile telephone platform could lower effort needed for application development and increase information exchange. Aanensen et al. (2009) developed a generic application for smartphones that also included digital photography as part of the mobile mapping.

In this article we focus on two relatively new information technology standards; the World Wide Web Consortium (W3C) Geolocation specification and the Open Geo-spatial Consortium (OGC) Web Processing Service. We discuss how these standards can contribute to risk reduction. Based on the former standard we present one new Web-tool for online pest field mapping of plant pests and host plants, while for the latter standards we discuss the potential and opportunities offered for prediction of future pest establishment. Geoport, the new Web-tool reported here, has also been tested to work directly towards biodiversity databases and the biodiversity data standard "Darwin Core." This data standard was proposed by the community of end-users and has been widely implemented, thereby providing volumes of data to better reveal global patterns of biodiversity (Wieczorek et al. 2012). Such information is fundamental to protect biodiversity. These examples demonstrate how information technology might serve to reduce the risks from pests and forms a new foundation for further development.

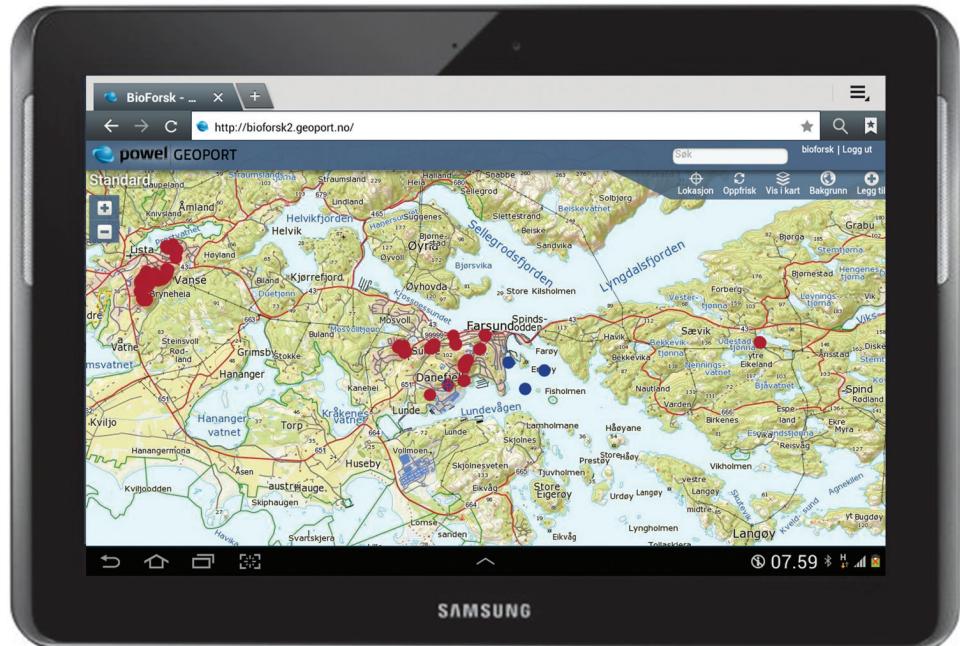
Applying information technology standards in Geoport – a Web tool example

The W3C-geolocation specification and support for its Application Programming Interface (API) were implemented in most Internet browsers after its publication. For mobile network devices having an Internet browser, like smartphones and tablet computers have, the result of such an implementation is standardized and simplified access to location information. By pointing the Internet browser to a certain Web-address that makes use of the W3C-geolocation functionality, providing direct access to the GPS hardware chip device for a Web-application, the user can immediately start to do online data recording to central storage from the field. In order to secure privacy, it is a compulsory part of the standard that the user always is asked for permission to allow the Web-page/Web-application access to the location information. The ease of access to Web-based user location information was the single most important factor triggering our initiative to expand on our previous work on network-linked field tools for online pest data recording (Rafoss et al. 2010). While the SMILEX application utilized one information technology standard to dynamically construct the user interface based on the remote source it was configured to record data against (Rafoss et al. 2010), the W3C-geolocation standard allows for the whole application to be distributed over a network. A Web-application for mapping of plant pests utilizing this opportunity is presented in this article. We followed a generic approach where an application previously used only for desktop Web map display and manual recording of pest data (Gyland et al. 2007) was extended with data recording functionality. The product is named Geoport and is based on the open source JavaScript library OpenLayers (Fig. 1A).

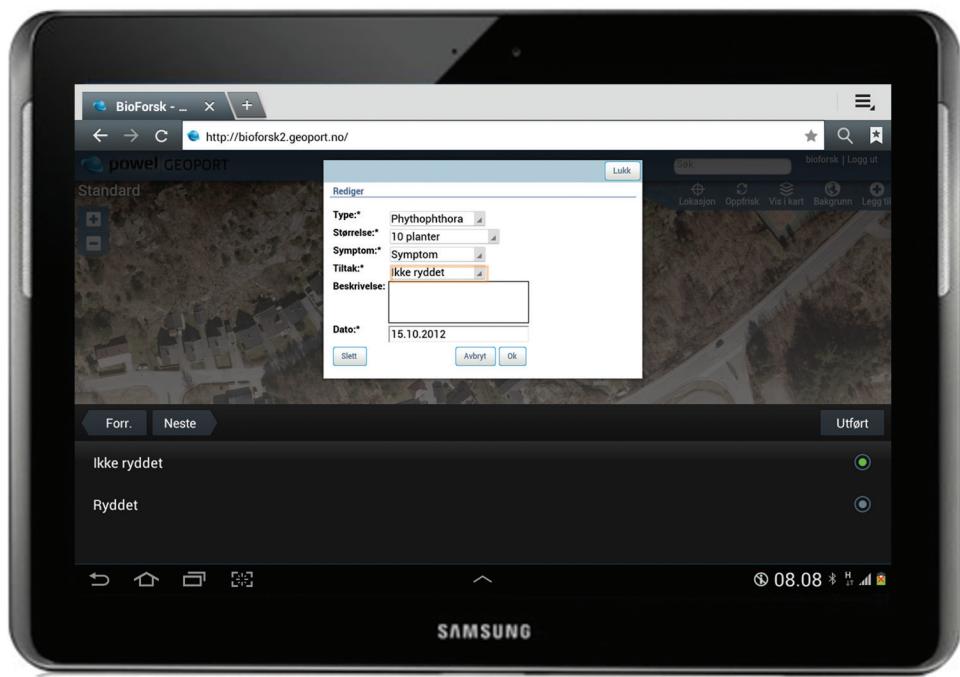
Geoport support for the W3C-geolocation specification and the Geolocation API standard

According to Popescu (2012), the Geolocation API “*defines a high-level interface to location information associated with the device hosting the implementation, such as latitude and longitude. The API itself is ignorant of the underlying location information sources. Common sources of location information include Global Positioning System (GPS) and location inferred from network signals such as IP address, RFID, WiFi and Bluetooth MAC addresses, and GSM/CDMA cell IDs, as well as user input*”.

Geolocation based on GPS signals regularly involves two sources of accuracy error under field conditions: (1) local reflection of GPS signals from large objects like buildings or trees, that can be falsely recorded by the GPS device and (2) error in the signal emerging from variation in solar activity that distort the GPS signals as they pass through the Earth’s ionosphere. In the situation where large objects in the vicinity affect the accuracy of signals, the user can intervene by switching to an aerial photography background map and then directly assessing the accuracy by comparing the physical surroundings to what is shown on the aerial photo around the position indicator.



A



B

Figure 1. Geoport displayed in an Internet browser running on a tablet. Upper figure shows existing mapped data on top of a topographic map, while the lower figure shows the dialog for registering new data, with background map switched to aerial imagery (orthophoto).

Moreover, in such situations the application can be set to allow the user to manually position the data recording in the map. For the second source of error, correction services delivered by various commercial suppliers improve accuracy down to the decimetre or centimetre or centimeter level. Such correction information was once available only for advanced GPS receivers equipped with an additional radio receiver, as these correction signals were disseminated along FM-radio channel signals. However, in recent years, these correction signals have also started to be disseminated over the mobile telephone network. This new option was considered to be implemented as an additional functionality of Geoport, but would have required programming of an additional software module that is not part of the Geolocation API standard to handle the signal code. To obtain this kind of increased accuracy, users would be required to buy access to such services from national suppliers. Although we considered the availability of GPS correction signals within the mobile network signal to be an interesting new option, we decided not to implement support for it in the current version. For the purpose of recording field data on pests, the position accuracy of 3–4 meters typically obtained when the solar activity is the only source of distortion, was considered sufficiently accurate. The quality of the hardware and the positioning averaging algorithms implemented by the hardware vendor can also affect position accuracy. However, based on our experience with smartphones and tablets from different main producers, all current technologies provide adequate position accuracy. The Geolocation API itself has an optional parameter “enableHighAccuracy” in the set of instructions for position acquisition. This attribute is implemented in the API to provide a hint that the application would like to receive the best possible results. Another intended purpose of this attribute is to allow other applications to inform the Geolocation application that they do not require high accuracy geolocation information, therefore, the implementation can avoid using geolocation components (e.g., GPS) that consume a significant amount of power. For Geoport we chose to activate the “enableHighAccuracy” option by default in order to ensure that the device always provided the most accurate position it is able to deliver, although this results in the slowest response times and largest power consumption. One alternative not yet enabled in the current version of Geoport is to allow the user to switch on and off this “enableHighAccuracy” parameter, which in practice would mean to make more use of the manual placement option based on high quality aerial map background. However, this will break with some of the automatic quality control principles of this data collection principle where time and space attributes of the data recording could be set by the system without the user being able to manipulate them.

Geoport support for the OpenGIS® Web Feature Service Interface and the Web Map Service Interface

Based on our previous experiences with OpenGIS® Web Feature Service Interface Standard (WFS) we chose to design the Geoport web application to allow data recording against any data source supporting Web Feature Service Transaction (WFS-T).

There are now several software products, both commercial and open-source based, supporting WFS-transactions (e.g. GeoServer, TinyOWS and ArcGIS Server) with most kinds of geographical data sources like file-based formats (e.g. ESRI Shape files) or database servers with support for geographic data types (e.g. PostgreSQL/PostGIS, Oracle Spatial, ArcSDE). In the following section, we introduce some of the technical principles to facilitate flow of species data records over the Internet, and furthermore, how eventually new data records can be used to trigger events like pest management actions or pest risk assessment re-analysis.

According to the OGC (Vretanos 2005), the OpenGIS® Web Feature Service Interface Standard (WFS) defines: “*interfaces for data access and manipulation operations on geographic features using HTTP as the distributed computing platform. Via these interfaces, a web user or service can combine, use and manage geodata -- the feature information behind a map image -- from different sources by invoking the following WFS operations on geographic features and elements:*”

- *Create a new feature instance*
- *Delete a feature instance*
- *Update a feature instance*
- *Lock a feature instance*
- *Get or query features based on spatial and non-spatial constraints*”

A subset of the above described operations of the WFS specification has been named as Web Feature Service Transactions or WFS-T in abbreviated form. The subset of the first four operations listed above constitutes the necessary operations to allow for full editing functionality for geospatial data over the Internet. While the WFS provide the information behind maps, and no map images, the OpenGIS® Web Map Service Interface Standard (WMS) does provide map images that also could be transparent to combine map layers from one or multiple servers (de la Beaujardiere 2006). Also WMS uses the hypertext transfer protocol (HTTP) of the Internet, but here the role of the protocol is just to transfer images over the Internet similar to how photos appearing in a Web-based newspaper, but with the addition that they are accompanied by information on how the images could be arranged in a (geographical) coordinate system to present a geographical map to the reader.

Workflow in Geoport

In order to allow different functionality, we decided to implement two modes of operation of Geoport on two different network addresses. One mode allowed the user to control placement of field recordings on the map. In this mode, GPS information is used to centre the map on the device only and the geographical coordinates for data recording are captured where the user taps to insert a new data point. A second mode had no option for user interaction except from placement of the mapping device itself

(smartphone or tablet) at the position of the point of interest. In this mode the geographical coordinates for data recording are taken directly from the GPS when a new data point is recorded. The former mode is desirable when positions of interest are difficult to access, e.g. in wetlands (bogs, lakes etc), while the benefit of the latter mode is that data are collected where the device is located.

A mapping session with the Geoport Web application initiates by starting up an Internet browser on the tablet or smartphone and then by entering the Web address. While there is no need for manual installation beforehand like for native applications, successful loading of the application requires network connection. After loading the application the user is asked to allow sharing of the geographical position. This is an integrated part of the W3C-geolocation specification to protect privacy. The user can respond to the request either by sharing the geographical location information once for the actual application session or for future application sessions or to not share the location information (for which the latter option prohibits the application from proceeding into a mapping session). In the mapping session previously registered data is shown by Style Layer Descriptors (SLD) on top of a background map (Fig. 1A) that could be switched between topographic or aerial imagery (orthophoto). The previously collected data shown in the map is coming directly as WFS data from the same data source as the data collection is operating. Background maps are delivered over a WMS service. To record new data, the user taps the “+” button which brings up a user dialog with predefined menu options for “type of registration”, “quantity”, “symptom”, “action taken” and a free text field for comments (Fig. 1B). The date and geographical coordinates are captured automatically from the device. The final action for the user to complete is to press “OK” which fires the WFS transaction. The WFS server then feeds back a message telling the user whether the data was safely secured at the server or not. The application returns to normal mapping mode at the current position.

Field use experiences

This Web application, run from a tablet device, offered several advantages for field data collection over handheld GPS-devices or first generation smart mobiles without touch screen. Tablets have much greater battery capacity than mobile phones, and the battery will not run out during the working day. The relatively large screen on a tablet also provided a better overview of data collected and map information. Fine details in the high quality background maps and aerial imagery provided by the Norwegian Mapping Authority become evident on the larger tablet screen. The detailed information on surroundings and the good overview is helpful in the working situation. Use of the touch screen was also more convenient on the tablet compared to the smartphone because the symbols were larger and easier to tap (although this could be adjusted at the expense of visible map information).

Geoport can in principle be used anywhere in the world. It can be configured to use any background map layers as long as they are available over the WMS standard

or the other Internet-based map distribution formats supported by the OpenLayers library. It has been tested in various parts of the world when configured to use map layers offered by Google's Google Maps service. For use in Norway, we chose to use the map services offered by the Land Registry and Cadastre (STATKART) as they offer the highest quality maps and aerial imagery for Norway. Geoport is not publically accessible as it is now distributed as a commercial product from the private company Powel based in Norway. However, the software on which Geoport is based, OpenLayers, is publically accessible as it is published as an “open source” software library at <http://openlayers.org>.

The greatest use of Geoport so far has been in the on-going nation-wide survey and eradication campaign in Norway against the plant pathogenic bacterium *Erwinia amylovora* which causes fire blight in pears, apples and some other members of the family Rosaceae (Rafoss et al. 2010). In 2012, a total of 15,458 host plant locations were inspected and mapped/remapped, distributed in 13 counties and 100 municipalities of Norway (Melbøe et al. 2013). In the survey all host plants were checked for symptoms of fire blight. The disease has not yet spread to the main fruit growing areas of Norway. The action taken depends upon which of the three zone status declared: “eradication zone”; “observation zone” or “protected zone”. An eradication zone is declared anywhere fire blight has been detected and all diseased plants are removed. As a preventive measure the most susceptible host plants are also removed. In the observation zone fire blight has not yet been detected. The observation zone borders the eradication zone, and the surveillance activity is systematic and extensive. In the protected zone, fire blight has not been detected and surveillance in this zone is at random.

The geoport application has also been successfully used at a smaller scale to register vascular invasive plants in Norway and to record data in agricultural fields in India.

Future standardization of geospatial pest risk analysis procedures and the OpenGIS® Web Processing Service

In the context of risk assessment and risk management of pests, geospatial information standards that can facilitate development of new knowledge from collected species occurrence data should be of high interest. The various approaches and algorithms developed to project whether species can establish and spread into novel areas based on the species' current distributions (see Elith and Leathwick 2009; Austin 2007 for a couple of reviews) are increasingly being compared (Elith et al. 2006; Dupin et al. 2011) or used in combination (Smolik et al. 2010). Furthermore, requests for early detection of emerging risks (EFSA 2011) as well as more robust predictions of pest establishment potential for novel areas can be expected. Automatic execution of species distribution models when new data are collected and multi-model operations, respectively, are approaches that could address these two needs. However, there is currently no existing service to tackle these challenges. This is where the OpenGIS® Web Processing Service (WPS) can play a role as a suitable standardization initiative.

According to the specification of OpenGIS® Web Processing Service edited by Schut (2007): “*WPS defines a standardized interface that facilitates the publishing of geospatial processes, and the discovery of and binding to those processes by clients. “Processes” include any algorithm, calculation or model that operates on spatially referenced data. “Publishing” means making available machine-readable binding information as well as human readable metadata that allows service discovery and use. A WPS can be configured to offer any sort of GIS functionality to clients across a network, including access to pre-programmed calculations and/or computation models that operate on spatially referenced data. A WPS may offer calculations as simple as subtracting one set of spatially referenced numbers from another (e.g., determining the difference in influenza cases between two different seasons), or as complicated as a global climate change model. The data required by the WPS can be delivered across a network, or available at the server. This interface specification provides mechanisms to identify the spatially referenced data required by the calculation, initiate the calculation, and manage the output from the calculation so that the client can access it*”.

Based on this definition, the WPS standard should have a potential to act as a framework for future standardization of the various modelling approaches applied to predict the potential for pest establishment and spread. Analysis of geospatial data is commonly associated with some technical burden to handle coordinate systems and projections properly. Further technical complexity is included when the time dimension is added to the analysis of species occurrence data. If standards are used and supported by the tools for analysis and prediction of species distribution, the management and processing of such data could be eased, which will allow the biologist or pest risk analyst to concentrate more on advancing the science and less on overcoming technical barriers.

Taking action - chaining of Web services

An earlier Norwegian study on the use of standardized information technology for risk management of pests, demonstrated the potential for chaining of Web-services for automatic warning messaging to be sent to potentially affected farmers and other stakeholders, based on events registered into a Web-client developed for the desktop office computer (Gyland et al. 2007). With the current tool for smartphones and tablet computers, this system is now in principle available for use from the field.

In a risk assessment context, server side routine checks could be set up on the in-coming pest data that could trigger pest risk analysis, or re-analysis, when the new data fulfil certain criteria identifying a potential emerging risk. The new abilities to constantly update field data could generate potential for a new level of immediacy not previously seen in the process of pest risk modelling. In order for this to be a new feature of the pest risk assessment process, risk assessment routines must be dynamically linked to the species presence/absence databases in a way that re-analysis could easily be invoked or even automatically triggered when new data are accumulated. If species distribution models were available as WPS services, we might experience similar effects

of lowered effort needs following from standardization as reported for field data collection in this article and by Rafoss et al. (2010).

Chaining (linking) species distribution models to species distribution databases by standards support may also further facilitate the step from assessment to management. Pest risk management procedures, e.g. emergency warnings and contingency plans, could be held up-to-date from risk assessment model based knowledge on range expansion of pests and associated scientific advice.

Discussion

There is little doubt that the current processes of globalization of trade in agricultural commodities and climate change are speeding up the rate of change in both natural- and agro-ecosystems. The risks emerging from these changes to food security and biodiversity are well documented. The role of technology in mitigating these risks needs as a general topic is beyond scope of this paper, but our study shows how technology can aid in keeping track of these changes and how principles of standardization can reduce the effort needed to put together efficient tools to track and potentially eradicate pests. Most of the mapping software coming with smartphones and tablets today readily allows field data collection. However, these tools normally allow little customization and standards support, even in their accompanying APIs that are offered to give more flexibility. Typically these applications cannot be customized to capture desired attributes and not configured to operate against user-defined data stores. The amount of information that should be collected while in the field is another interesting aspect that deserves discussion. On one hand, ideally it should handle all the information fields that are required for a biodiversity record according to the biodiversity data standard “Darwin Core”, e.g. see Wieczorek et al. (2012) for a description. Many parts of that standard can actually be effectively handled by metadata settings on the database side (e.g., information about the identity of the registering organization and the person responsible for species identification). On the other hand, the biodiversity data standards are created from a nature conservation perspective and may therefore not contain all information elements that are of interest for pest risk management, such as “symptoms” or “action taken”.

Another aspect that is highly relevant from a pest risk assessment perspective is the use of such tools to document true absence of species. In combination with a robust predefined sampling strategy, the tool described in this paper should have a great potential to improve the availability of true absence data that generally are scarce. Combining the predefined sampling strategy with citizen science is another interesting opportunity that potentially could generate high interest and high utility for pest risk assessment and management. Scientists could take advantage of the fact that smartphones and tablets lend themselves to provide guidance to the citizen science by combining text and multimedia and thereby improve the quality of the information

collected by the public. This could be one way to alleviate the general scarcity of true absence data by use of modern technology and society involvement.

For the future we would like to see expansion of functionality to define new data sources from the field by having a user interface that automatically configures and set up new remote data sources that can be initiated to receive field data. At present, functions that allow creation of new data stores are not covered by any of the standards for geospatial information. We would also like to see good functionality to handle absence data for species distribution mapping.

Conclusion

Smartphones and tablets are now readily available and their costs are going down. Based on an open source JavaScript library and utilization of open standards for geo-spatial information, the Geoport Web-application offers a platform independent tool for field data collection with a great potential to fight the risks posed by pests to food security and biodiversity. As location based technology and informatics help to simplify the collection of pest data, we recommend that pest risk analysts should make greater use of innovations in geospatial information technology and standards. Species distribution models should be linked to species distribution databases, e.g. as chained WPS services that could be triggered by new pest data occurrences according to certain criteria and thereby warn about potentially emerging risks. Detection of emerging risks at an early stage by automatic triggering of prediction algorithms when a species appear outside its currently known distribution range can allow for earlier action and thereby reducing risks from pests.

References

- Aanensen DM, Huntley DM, Feil EJ, al-Owain F, Spratt BG (2009) EpiCollect: linking smartphones to web applications for epidemiology, ecology and community data collection. PLoS ONE 4(9): 1–7. doi: 10.1371/journal.pone.0006968
- Austin M (2007) Species distribution models and ecological theory: A critical assessment and some possible new approaches. Ecological Modelling 200(1–2): 1–19. doi: 10.1016/j.ecolmodel.2006.07.005
- Baker R, Cannon R, Bartlett P, Barker I (2005) Novel strategies for assessing and managing the risks posed by invasive alien species to global crop production and biodiversity. Annals of Applied Biology 146: 177–191. doi: 10.1111/j.1744-7348.2005.040071.x
- de la Beaujardiere J (2006) OpenGIS® Web Map Server Implementation Specification. Open GIS Consortium Inc. OGC® 06–042.
- Dupin M, Reynaud P, Jarošík V, Baker R, Brunel S, Eyre D, Pergl J, Makowski D (2011) Effects of the Training Dataset Characteristics on the Performance of Nine Species Distribu-

- tion Models: Application to *Diabrotica virgifera virgifera*. PLoS ONE 6(6): e20957. doi: 10.1371/journal.pone.0020957
- EFSA (2011) Scientific Colloquium on Emerging Risks in Plant Health: from plant pest interactions to global change Summary Report EFSA Scientific Colloquium 16, 9–10 June 2011, Parma, Italy.
- Elith J, Graham CH, Anderson RP, Dudi'k M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JMcC, Peterson AT, Phillips SJ, Richardson KS, Schachetti-Pereira R, Schapire RE, Sobero'n J, Williams S, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151.
- Elith J, Leathwick JR (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697. doi: 10.1146/annurev.ecolsys.110308.120159
- Gyland LF, Bø T, Aronsen JE, Engravslia L, Flage LM, Sørensen S, Damgaard A (2007) SMARTRAP–Sluttrapport–Sekvensiell kjeding av WebServices i system for beredskaps-/katastrofehåndtering i Mattilsynet. [In Norwegian] http://norgedigitalt.no/Norge_digitalt/Norsk/Prosjekter/Smartrap/filestore/Norge_Digitalt_ny/Prosjekter/Smartrap/SMARTRAP_Sluttrapport_071023.pdf
- Melbøe N, Sletten A, Talgø V, Rafoss T, Perminow JIS (2013) Rapport om overvåking, kartlegging og bekjempelse av pårebrann i 2012. Report, Norwegian Food Safety Authority, February 2013. [In Norwegian with English abstract]
- Mooney HA, Hobbs RJ (2000) Invasive Species in a Changing World. Island Press.
- Popescu A (2012) Geolocation API Specification. Editor's Draft (for W3C Proposed Recommendation), May 2012. <http://www.w3.org/TR/2012/PR-geolocation-API-201205/> [accessed 2012-09-26]
- Rafoss T, Sælid K, Sletten A, Gyland LF, Engravslia L (2010) Open geospatial technology standards and their potential in plant pest risk management – GPS enabled mobile phones utilizing Open geospatial technology standards Web Feature Service Transactions support the fighting of fire blight disease in Norway. *Computers and Electronics in Agriculture* 74 (2): 336–340. doi: 10.1016/j.compag.2010.08.006
- Schut P (2007) OpenGIS® Web Processing Service. Open GIS Consortium Inc. OGC 05-007r7
- Smolik MG, Dullinger S, Essl F, Kleinbauer I, Leitner M, Peterseil J, Stadler L-M, Vogl G (2010) Integrating species distribution models and interacting particle systems to predict the spread of an invasive alien plant. *Journal of Biogeography* 37: 411–422. doi: 10.1111/j.1365-2699.2009.02227.x
- Vretanos PA (2005) Web Feature Service Implementation Specification. Open GIS Consortium Inc., OGC 04-094.
- Wieczorek J, Bloom D, Guralnick R, Blum S, Döring M, Giovanni R, Robertson T, Vieglaiset D (2012) Darwin Core: An Evolving Community-Developed Biodiversity Data Standard. PLoS ONE 7(1): e29715. doi: 10.1371/journal.pone.0029715

Incorporating climate change into pest risk models for forest pathogens: a role for cold stress in an era of global warming?

Robert C. Venette¹

¹ USDA, Forest Service, Northern Research Station, St. Paul, MN 55108, USA

Corresponding author: Rob Venette (rvenette@fs.fed.us)

Academic editor: Roger Magarey | Received 26 September 2012 | Accepted 1 July 2013 | Published 13 September 2013

Citation: Venette RC (2013) Incorporating climate change into pest risk models for forest pathogens: a role for cold stress in an era of global warming? In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 131–150. doi: 10.3897/neobiota.18.4047

Abstract

Climate change may alter the distribution and activity of native and alien pathogens that infect trees and, in severe cases, cause tree death. In this study, potential future changes in climate suitability are investigated for three forest pathogens that occur in western North America: the native *Arceuthobium tsugense* subsp. *tsugense*, hemlock dwarf mistletoe, and two alien invasive species, *Dothistroma septosporum*, the cause of red band needle blight or Dothistroma needle blight, and *Phytophthora ramorum*, the cause of sudden oak death or ramorum blight. Specifically, the software CLIMEX is used to calculate Cold-Stress, Heat-Stress, and Dry-Stress indices for each pathogen in 98,224 grid cells in North America. Downscaled climate projections from the general circulation models CGCM1, CSIRO Mk2, and HadCM3 drive forecasts for 2020, 2050 and 2080. These climate projections are then analyzed to forecast shifts in the geographic extent of abiotic stresses that are severe enough to directly kill pathogen propagules and prevent year-round establishment of these pathogens. Cold stress currently has a major impact on climate suitability for all three pathogens; heat stress is likely to become more significant in the future. I forecast that the geographic extent of cold stress will decline from its current levels by a constant 5% ($\pm 1\%$) of all grid cells in each 30-yr projection horizon for all three pathogens. Forecasts suggest the extent of heat stress will increase concurrently by 4% ($\pm 1\%$) in each 30-yr projection horizon. Drought stress shows no consistent trend over time. No disproportionate effect of climate change on the two alien invasive pathogens over the native is forecasted. These results suggest that forecasts of future climate suitability for pathogens based on historical climate normals are accurate for less than 30 yrs. Adaptive management strategies in forestry will be needed to respond as these changes unfold.

Keywords

Sudden oak death, red band needle blight, hemlock dwarf mistletoe, CLIMEX, alien invasive pathogens, exotic species

Introduction

Trees play pivotal roles in global carbon cycles. They remove significant amounts of carbon from the atmosphere annually and sequester fixed carbon for long periods (Bonan 2008; Chazdon 2008). Tree diseases can interfere with these processes. Disease, i.e., abnormal physiological function, in plants is the consequence of the interaction of a virulent pathogen with a susceptible host and a conducive environment. Forest health protection is a key strategy to adapt to climate change (e.g., Spittlehouse and Stewart 2003) and to ameliorate atmospheric carbon levels (Canadell and Raupach 2008; Nabuurs et al. 2007).

Climate change portends significant shifts in the structure and function of forests. In particular, ecological niche models for a number of tree species suggest future areas of climatic suitability will shift polewards in response to changes in temperature and moisture (Iverson et al. 2008; McKenney et al. 2011). For many species in general, dispersal capacity, demographic stochasticity, and cold-induced mortality are likely to dominate population processes at the leading, or expanding, edge of the range shift (Hampe and Petit 2005). At the rear, or contracting, edge, drought stress and genetic drift are likely to be among the dominant processes (Hampe and Petit 2005). Severe heat and drought events in western North America and elsewhere in the world already may have contributed to widespread tree mortality (Allen et al. 2010; van Mantgem et al. 2009).

Though climate change may be the ultimate cause of tree death, the proximate cause may be the activity of insects and diseases (Sturrock et al. 2011). Just as trees have specific temperature and moisture requirements, so do most pathogens. Qualitative assessments suggest that many forest diseases whose dynamics are directly governed by weather (e.g., *Phytophthora* root rot, *Dothistroma* needle blight, or Swiss needle cast) will become more severe if climate becomes warmer and wetter and less severe if conditions are warmer and drier (Kliejunas 2011; Sturrock et al. 2011). In contrast, diseases whose dynamics are mediated primarily by host condition (e.g., *Armillaria* root disease, *Botryosphaeria* canker, or pitch canker) will worsen if conditions become warmer and drier and will generally be unaffected if climate is warmer and wetter (Kliejunas 2011; Sturrock et al. 2011). Such qualitative assessments acknowledge substantial uncertainty as a result, in part, of a poor understanding of the epidemiology of many diseases, an inexact course of future climate change, and regional variation in the pattern and extent of climate changes (Boland et al. 2004; Dukes et al. 2009; Hepting 1963; Sturrock et al. 2011).

A general concern about the interaction of climate change and invasive alien species continues to grow (Driscoll et al. 2012; Dukes and Mooney 1999; Smith et al.

2012). Many invasive species are known to have broad environmental tolerances and high dispersal capacity. As a result, alien species effectively may be “pre-adapted” to future climate conditions and poised to dominate native species (Dukes and Mooney 1999). The potential significance of climate change for invasive alien pathogens of trees remains to be tested.

Pest risk maps illustrate how the likelihood and consequence of invasion by an alien species varies spatially within an area of concern (Venette et al. 2010). For many insects, weeds, and pathogens, this variation is likely to be driven, in part, by local and regional differences in temperature and precipitation. Some pest risk maps focus on an analysis of climatic suitability to characterize where an invasive alien species might become established if it were to arrive in an area, relying on the logical argument that there will be no impact if there is no establishment. If the forecast is driven by climatic normals, the resulting pest risk map will only be relevant in the future if temperature and moisture continue to fluctuate as they have for the previous 30 years. Pest risk maps would be substantially improved if they incorporated effects of climate change (Venette et al. 2010).

A number of analysts have incorporated climate change into forecasts of future climate suitability for invasive alien species (e.g. Baker et al. 2000; Desprez-Loustau et al. 2007; Watt et al. 2009). The common approach is to gather information about known geographic occurrences and absences of a species and to integrate these points with a database of current climactic norms. Climatological dimensions of the ecological niche are inferred from these data, and this inference is compared with downscaled output from general circulation models to determine if an area might be climatically suitable for an alien species in the future.

The purpose of this study was to compare the potential effects of future climate change on population stresses experienced by three forest pathogens: *Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp *tsugense*, western hemlock dwarf mistletoe, hereafter simply *A. tsugense*; *Dothistroma septosporum* (Dorog.) Morelet, the cause of Dothistroma (or red band) needle blight; and *Phytophthora ramorum* Werres, de Cock & Man in't Veld, the cause of sudden oak death and ramorum blight. *Phytophthora ramorum* is an oomycete that can infect more than 100 plant species and is new to Europe and western North America (Rizzo et al. 2005). The geographic origins of the pathogen remain unknown (Grunwald et al. 2012). As of 2013, the pathogen was established in North America in southwest Oregon (Curry Co.) and northwestern California (13 counties) and recovered from streams in Mississippi, Alabama, Florida, Georgia, and North Carolina. *Dothistroma septosporum* is a fungus with a cosmopolitan distribution and generally occurs wherever its hosts, several pine species (*Pinus* spp.), occur (Farr et al. 1995), though a particularly severe epidemic is occurring in British Columbia (Woods et al. 2005). The pathogen may be native to high elevations in Central America (Evans 1984) or the Himalayas (Evans 1984; Ivory 1994). *Arceuthobium tsugense* is a parasitic plant that is native to western North America, specifically western British Columbia, Washington state, Oregon, and northern California (Hawksworth and Wiens 1996). This mistletoe commonly infects western hemlock, *Tsuga heterophylla*

(Hawksworth and Wiens 1996). Under appropriate conditions, each of these pathogens can kill its host. I hypothesize that if native species tend to be more adapted to specific environmental conditions than alien invasive species, future climate-induced stresses should be more severe in North America for the native *A. tsugense* than on either alien species, *D. septosporum* or *P. ramorum*. I further hypothesize that different general circulation models should yield equivalent estimates of climate induced-stress. Abiotic stresses particularly those resulting from cold, heat, and drought, that act directly on these pathogens are the focus of this paper because these stresses are likely to dictate climatic bounds on the occurrence of these pathogens.

Materials and methods

Climate data. Climate normals and output from general circulation models downscaled to 10 arc-minutes were obtained from Worldclim.org, specifically mean monthly minimum temperature, maximum temperature, and precipitation. Downscaling had been performed using ANUSPLIN (Hijmans et al. 2005). At a resolution of 10 arc-minutes, each grid was approximately 18.6×18.6 km at the equator. I obtained climate data for four projection horizons – current, 2020, 2050, and 2080 – from three general circulation models – CGCM1, CSIRO Mk2, and HadCM3 – under emission scenario b2a. This scenario assumes a low increase in greenhouse gas emissions with a corresponding increase in global average temperature of approximately 2°C by 2080. This change is less than changes suggested by other emission scenarios, but future climate is expected to change by at least this much. In total, data were procured for ten climate projections, i.e., three general circulation models x three projection horizons + current conditions. Current data primarily reflected the 30-yr climate normal from 1961–1990, though in some locations it may have reflected the period from 1950–2000 (Hijmans et al. 2005). There were 584,720 grid cells worldwide.

I restricted my analysis to North America, the only continent on which all three pathogens co-occur. Within the climate data sets, I functionally defined North America as those grid cells with centers occurring within the box with a northwest corner at 170°W and 80°N and a southeast corner at 50°W and 12°N . Individual grid cells were excluded from the analysis if projected minimum temperature was greater than the maximum temperature or if some climate data were missing. This standard ensured that exactly the same areas of North America were compared over time and left 98,224 grid cells for the continent. Data files were processed to be compatible with CLIMEX ver 2.0 (Hearne Scientific Software, South Yarra, Australia).

Estimation of abiotic stresses acting on pathogens. The “Compare Locations” feature of CLIMEX ver 2.0 was used to forecast physiological stresses experienced by *A. tsugense*, *D. septosporum*, and *P. ramorum* in response to extreme cold, heat, drought, and wetness now and in the future. CLIMEX calculated values for respective stress indices when temperatures or moistures exceeded species-specific thresholds. Stress also accumulated at species-specific rates. The final Cold-Stress, Heat-Stress, Dry-Stress, and

Wet-Stress indices potentially varied from 0 to 999. Values of 0 indicated no stress, and values of 100 indicated complete inoculum mortality from an abiotic agent. Values greater than 100 reflected severely stressful conditions (Sutherst et al. 2004). Grid cells with a stress index >99 were considered unsuitable for the year-round persistence of that pathogen. Sutherst and Maywald (1985) and Sutherst et al. (2004) provided specific formulas and details for the calculation of stress indices.

CLIMEX parameters for each species are reported in Table 1. CLIMEX parameters for *P. ramorum* were taken from Venette and Cohen (2006). Parameters for *A. tsugense* were developed through an iterative geographic fitting process initially described by Sutherst and Maywald (1985). The process began with a generic template for a temperate species. Geographic plots of CLIMEX indices were compared with the actual distribution reported by Hawksworth and Wiens (1996). I recursively modified CLIMEX parameters and compared with the known distribution until a qualitatively satisfactory fit was found.

CLIMEX parameters for *D. septosporum* were obtained from Watt et al. (2009) and modified slightly to reconcile with extant literature about the effect of heat on conidia viability. Gibson (1972) reported that conidia of what would now be recognized as *D. septosporum* could survive 9 wk at 30°C but only “several days” of dry heat at 35°C. I presumed that “several days” meant 6 days. Calculations based on these estimates indicated that heat stress would begin to accrue at 29.9°C, similar to the value from Watt et al. (2009), but the rate of stress accumulation would be 0.247 wk⁻¹. The modified parameter set qualitatively fit the distribution of *Dothistroma* reported by Watt et al. (2009).

Statistical analyses. All statistical analysis was performed in SAS 9.2 (SAS Institute, Cary, NC). Although individual grid cells are the observational units in this study, each observational unit is not independent in space. Thus, analyses focused on the propor-

Table 1. CLIMEX stress parameters for three forest pathogens.

Index	Parameter	<i>Arceuthobium tsugense</i>	<i>Dothistroma septosporum</i>	<i>Phytophthora ramorum</i>
Cold stress	TTCS=temperature threshold (°C)	-3.9	-30	-
	THCS=stress accumulation rate (wk ⁻¹)	-0.025	-0.05	-
	DTCS=degree-day threshold	-	-	15
	DHCS=stress accumulation rate (wk ⁻¹)	-	-	-0.0001
Heat stress	TTHS=temperature threshold (°C)	22	29.9	30
	THHS=stress accumulation rate (wk ⁻¹)	0.001	0.247	0.005
Dry stress	SMDS=moisture threshold [†]	0.3	0.10	0.2
	HDS=stress accumulation rate (wk ⁻¹)	-0.015	-0.005	-0.005
Wet stress	SMWS=moisture threshold [†]	2.5	-	2.5
	HWS=stress accumulation rate (wk ⁻¹)	0.002	-	0.002
Hot-wet stress	TTHW=temperature threshold (°C)	-	28°C	-
	MTHW=moisture threshold [†]	-	1	-
	PHW=stress accumulation rate (wk ⁻¹)	-	0.025	-

[†], Moisture is expressed as a proportion of moisture holding capacity with values of 1 equal to saturation. Values > 1 reflect flooded conditions.

tions of grid cells in North America in which CLIMEX indices of cold stress, heat stress, wet stress or drought stress were >99. A grid cell that met one of these criteria was projected to be inhospitable for the year-round presence of the pathogen. The emphasis on grid cells with stress >99 ignores cases in which an abiotic agent might cause partial mortality of the population, but allows the analysis to focus on clear potential shifts in the geographic range in which a pathogen might be forecast to persist year-round. I refer to these proportions as the extent of stress. – Wet stress in North America was always 0 for each of the pathogens under the current and future climate, so wet stress was not analyzed statistically.

The extent of each stress from 2020 to 2080 was found to be normally distributed (Univariate procedure in SAS 9.2) and was analyzed first with repeated measures analysis of variance (Mixed procedure in SAS 9.2). General circulation model ($n=3$) and year ($n=3$) were included as main effects with a first-order auto regressive term to account for temporal covariance in the data. The experimental design did not allow for the testing of an interaction between year and general circulation model. Differences among forecasts for 2020, 2050, and 2080 were estimated using Tukey's multiple comparison test of least-squares means with $\alpha = 0.05$. Two-tailed t-tests for the difference between a population mean and a hypothesized population mean to compare results from 2020, 2050, and 2080, the population means, with results for the current climate, the hypothesized population mean, because no statistical sources of variation existed for stress estimates based on current climate. A Bonferroni-adjustment of α was applied to correct for multiple comparisons and ensure an overall $\alpha = 0.05$.

To compare changes in the extent of each stress over time among pathogens, I used mixed model analysis for linear regression (Mixed procedure in SAS 9.2). A first-order autoregressive error structure was used to account for autocorrelation in observations over time. Factors in the regression were general circulation model ($n=4$, now including current), pathogen ($n=3$), and time ($n=4$). Time was measured in 30-yr projection horizons, with 0 corresponding to 1990, 1 corresponding to 2020, and so on. All observations from the same levels of each general circulation model and pathogen effectively represent a single subject. The analysis assumes independence of observations from different subjects. Degrees of freedom were determined using the Kenward-Rogers approach. Paired contrasts were used to test for different intercepts and slopes among regression lines for each pathogen. A Bonferroni-adjustment of α was applied to correct for multiple comparisons and ensure an overall $\alpha = 0.05$.

All maps were created in ArcMap 9.3 (ESRI, Redlands, CA). For each stress index at each projection horizon, a grid cell is assigned the median stress value forecasted from the three general circulation models.

Results

Effects of climate change on stress projections for each pathogen. CLIMEX models driven by downscaled output from general circulation models suggest the geographic extent

of cold stress for *A. tsugense* will diminish in time ($df = 2,4; F=24.52; P=0.006$) while the extent of heat stress will increase ($df = 2,4; F=103.22; P<0.001$). The extent of drought stress is projected to be greater than it is currently, but no different from 2020 through 2080 ($df = 2,4; F=1.13; P=0.408$). Approximately 78.7% of grid cells are currently too cold for *A. tsugense* to persist (Fig. 1A). These cells generally fall north of 37°N latitude but not along the East or West Coasts (Fig. 2). The extent of cold stress will be reduced by 2020 (Fig. 1A), then generally occurring north of 39°N latitude, remain relatively unchanged through 2050 and again decline by 2080, when cold stress will generally occur north of 40°N latitude (Fig. 2). Heat stress currently affects 23.2% of grid cells (Fig. 1A), generally south of 42°N latitude (Fig. 2). This stress will increase to 30.6% in 2020 (Fig. 1A), generally south of 43°N latitude (Fig. 2), and continue to increase by an average of 3% of all grid cells in each subsequent 30-yr projection horizon through 2080 (Fig. 1A), by which time heat stress is projected to be severe throughout most of Mexico and the contiguous United States (Fig. 2). Drought stress for *A. tsugense* currently affects 47.9% of all grid cells in North America, generally west of 96° W longitude (Fig. 2). This extent will increase to approximately 50.3% by 2020 and remain at this level through 2080 (Fig. 1A).

For *D. septosporum*, the future extent of cold stress in North America will diminish through time ($df = 2,4; F=59.12; P=0.001$) while the future extent of heat stress will increase ($df = 2,4; F=19.35; P=0.009$); forecasts suggest the extent of drought stress for this pathogen will not change ($df = 2,4; F=1.75; P=0.284$). Currently, 19.3% of grid cells are inhospitable to *D. septosporum* because of cold, greater than in any future 30-year projection horizon for this pathogen (Fig. 1B). These cells generally occur north of 62°N latitude (Fig. 3). In each subsequent projection horizon, about 5.0% of all grid cells will lose cold stress, so by 2080, only 4.2% of grid cells will be too cold for *D. septosporum* to remain viable year-round (Fig. 1B). These cells are projected to occur in northern Canada and Alaska (Fig. 3). Heat stress currently affects 18.4% of grid cells, less than in any future projection horizon (Fig. 1B), grid cells with a Heat Stress index > 99 occur generally south

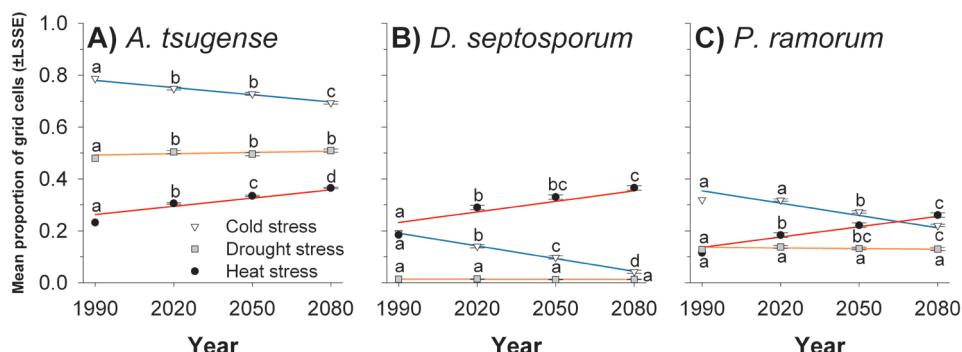


Figure 1. Proportion of North American grid cells with CLIMEX stress indices >99 over time for **A** *Arceuthobium tsugense* **B** *Dothistroma septosporum* and **C** *Phytophthora ramorum*. For each species, values for a stress with the same letter are not significantly different at $\alpha = 0.05$. Lines are predicted values from regression models described in Table 3. LSSE, least-squares standard error.

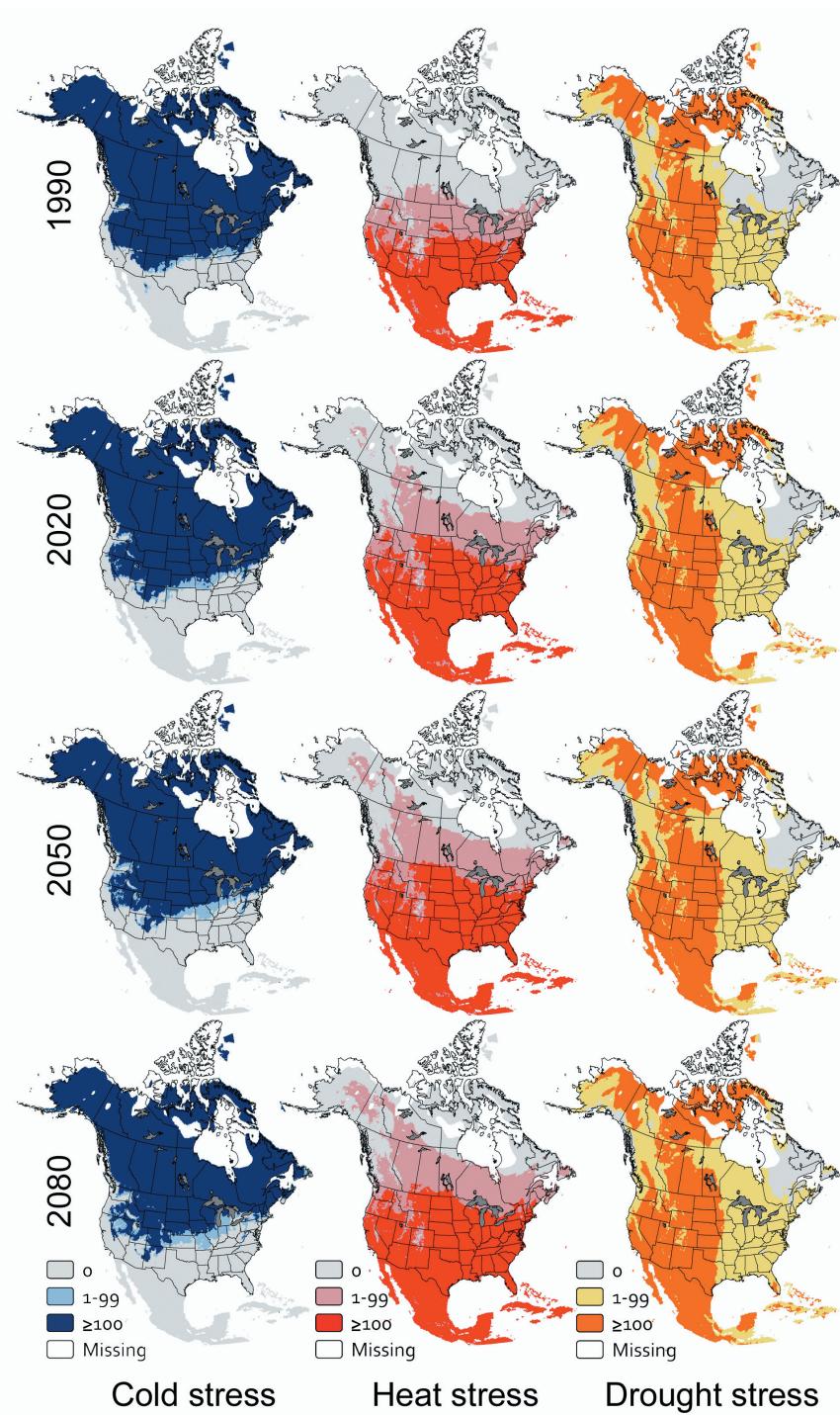


Figure 2. CLIMEX stress indices over time for *Arceuthobium tsugense* in North America.

of 37°N latitude (Fig. 3). The proportion of grid cells with heat stress will increase to 29.0% by 2020 and by an additional 3.8% of all grid cells in each subsequent projection horizon through 2080. By this time heat stress will extend throughout Mexico and the contiguous United States, except at high elevations and along the Pacific coast (Fig. 3). Drought stress is expected to affect approximately 1.3% of all grid cells now and through 2080, primarily in Baja California, Mexico and the desert Southwest, USA (Fig. 3).

For *P. ramorum*, the future geographic extent of cold stress will decline over time ($df = 2,4; F=93.57; P<0.001$) while the extent of heat stress will increase ($df = 2,4; F=19.04; P=0.009$). The extent of drought stress is not projected to change ($df = 2,4; F=0.54; P=0.619$). Currently, 31.9% of grid cells are too cold to maintain viable populations of *P. ramorum* year-round. These cells occur at high elevations and in northern portions of Canada and Alaska (Fig. 4). This extent of cold stress is forecasted to remain effectively unchanged through 2020. Then, the extent of cold stress will decline by 4-5% of grid cells in each subsequent 30-year projection horizon (Fig. 1C). By 2080, grid cells with a Cold Stress index > 99, will occur primarily in northern Labrador, northern Quebec, the Northwest Territories, the Yukon Territory, and northern Alaska (Fig. 4). Heat stress currently affects 11.5% of grid cells (Fig. 1C), generally south of 33°N latitude (Fig. 4). By 2020, the extent of heat stress is projected to increase to 18.4% of all grid cells and to continue to increase by approximately 4% of all grid cells in each subsequent projection horizon. By 2080, grid cells with a Heat Stress index > 99 will occur up to approximately 44°N latitude, except at high elevations (Fig. 4). Drought stress is expected to affect approximately 13% of all grid cells now and through 2080 (Fig. 1C), acting sporadically west of 99°W longitude (Fig. 4).

Effects of climate change on stress projections among pathogens. The three pathogens differed in the extent to which cold stress might currently constrain climate suitability for each species ($df = 1,12; F>34.38; P<0.001$ for three contrasts). The current extent of cold stress for *A. tsugense* is significantly greater than for *P. ramorum*, which itself has a greater extent of cold stress than *D. septosporum* (Table 3). The constant rate of change in the extent of cold stress over time was significantly less than 0 (Type 1 test of fixed effect of slope: $df = 3,6.83; F=22.90; P<0.001$), but did not differ among the three pathogens ($df = 1,6.83; F<2.90; P\geq 0.134$ for three contrasts).

The extent to which heat stress might currently limit climate suitability for *A. tsugense* or *D. septosporum* was greater than for *P. ramorum* (Table 3; $df = 1,12.2; F>12.2; P\leq 0.001$ for two contrasts), but the extent of heat stress that might currently act on *A. tsugense* was not different from that extent for *D. septosporum* ($df = 1,12.2; F=1.74; P=0.211$). The constant rate of change in the extent of heat stress over time was significantly greater than 0 (Type 1 test of fixed effect of slope: $df = 3,18.8; F=45.30; P<0.001$), but did not differ among the three pathogens (Table 3; $df = 1,18.8; F<1.32; P\geq 0.265$ for three contrasts).

The three pathogens differed in the extent to which drought stress might currently limit climate suitability of each species ($df = 1,18.8; F>18.8; P<0.001$ for three contrasts). The extent of drought stress was greater for *A. tsugense* than *P. ramorum*, which in turn had a greater extent of drought stress than *D. septosporum*. The constant rate of

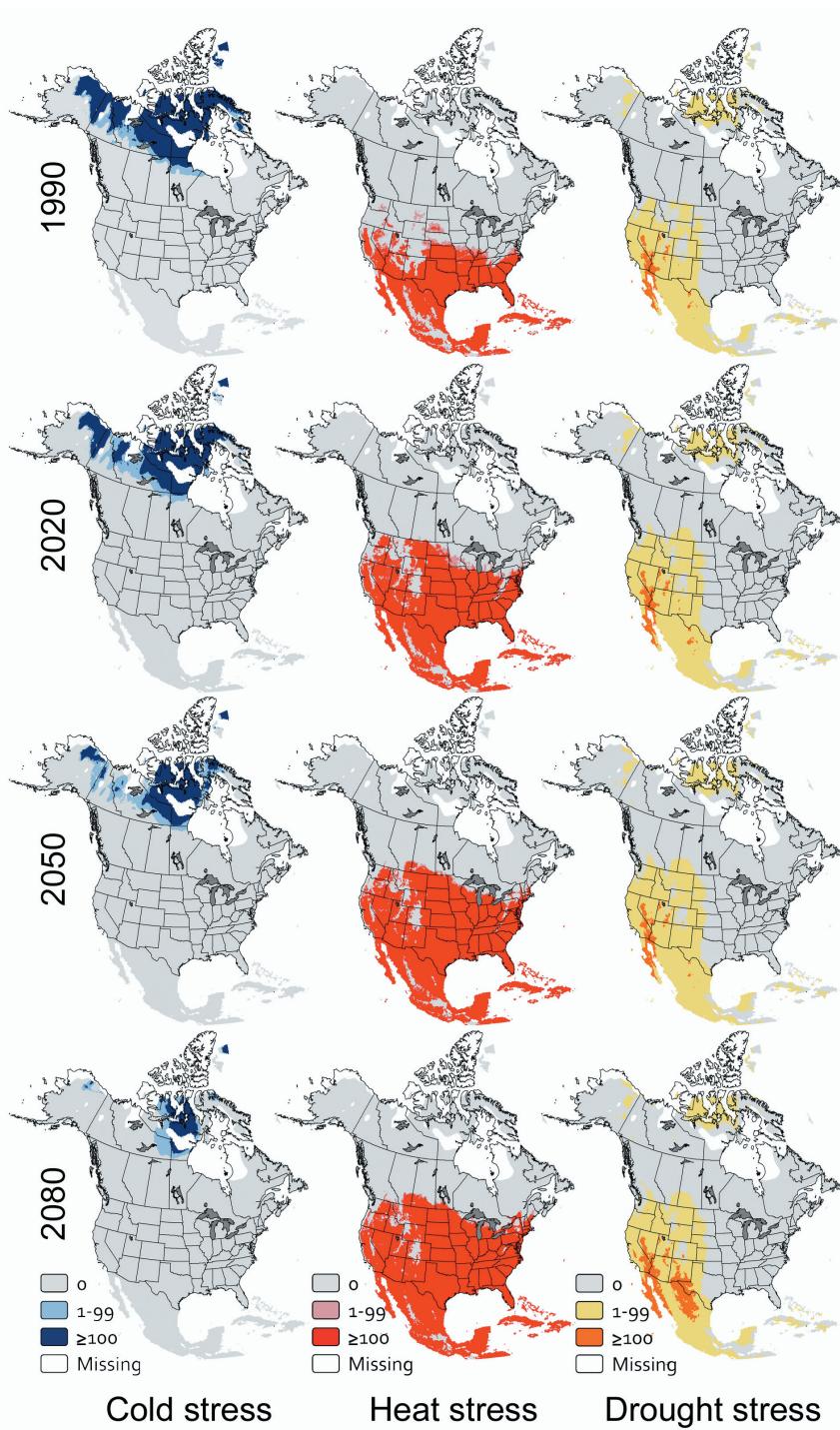


Figure 3. CLIMEX stress indices over time for *Dothistroma septosporum* in North America.

change in the extent of heat stress over time did not differ among the three pathogens ($df = 1,23.8$; $F \leq 1.65$; $P \geq 0.361$ for three contrasts) and was not different from 0 (Type 1 test of fixed effect of slope: $df=3,23.8$; $F=0.61$; $P=0.614$).

Effects of different general circulation models on stress projections for each pathogen. For *A. tsugense*, different general circulation models yielded different estimates of the future extent of cold stress ($df = 2,4$; $F=13.57$; $P=0.016$), heat stress ($df = 2,4$; $F=12.52$; $P=0.019$), and drought stress ($df = 2,4$; $F=12.81$; $P=0.018$). HadCM3 gave a greater extent of cold stress than CGCM1 or CSIROmk2; the extent of cold stress for *A. tsugense* forecasted from CGCM1 and CSIROmk2 were similar (Table 2). CGCM1 gave a lesser extent of heat stress than CSIROmk2 or HadCM3; the extent of heat stress from CSIROmk2 and HadCM3 were similar. Forecasts of the extent of drought stress based on CGCM1 were greater than HadCM3, but such forecasts based on CSIROmk2 were not different from either of the other general circulation models.

Different general circulation models yielded different estimates of the extent of cold stress for *D. septosporum* ($df = 2,4$; $F=22.08$; $P=0.007$) and *P. ramorum* ($df = 2,4$; $F=93.57$; $P<0.001$). For both pathogens, CSIROmk2 climate projections gave lower forecasts of the extent of cold stress than did CGCM1 or HadCM3 (Table 2). Though different general circulation models gave different estimates of the extent heat stress for *D. septosporum* ($df = 2,4$; $F=9.30$; $P=0.031$), they did not differ for *P. ramorum* ($df = 2,4$; $F=5.83$; $P=0.065$). For *D. septosporum*, the extent of heat stress based on CSIROmk2 was greater than the extent based on CGCM1; the projected extent of heat stress based on HadCM3 was not different from the other two general circulation models (Table 2). Estimates of the future extent of drought stress did not differ among general circulation models for *D. septosporum* ($df = 2,4$; $F=4.47$; $P=0.102$) or *P. ramorum* ($df = 2,4$; $F=1.65$; $P=0.300$).

Table 2. Effect of general circulation models on extent of forecasted abiotic stresses for three forest pathogens[†].

Species	General circulation model	Cold stress (%±LSSE) [‡]		Heat stress (%±LSSE)		Drought stress (%±LSSE)	
<i>Arceuthobium tsugense</i>	CGCM1	71.6±0.6	A	32.3±0.3	A	52.5±0.6	A
	CSIROMk2	70.8±0.6	A	34.0±0.3	B	50.4±0.6	AB
	HadCM3	74.7±0.6	B	34.2±0.3	B	48.0±0.6	B
<i>Dothistroma septosporum</i>	CGCM1	9.7±0.6	A	30.0±0.9	A	1.1±0.1	A
	CSIROMk2	6.2±0.6	B	35.0±0.9	B	1.4±0.1	A
	HadCM3	12.1±0.6	A	33.6±0.9	AB	1.4±0.1	A
<i>Phytophthora ramorum</i>	CGCM1	29.6±0.5	A	20.0±0.9	A	14.1±0.6	A
	CSIROMk2	21.8±0.5	B	22.3±0.9	A	12.7±0.6	A
	HadCM3	29.8±0.5	A	24.2±0.9	A	13.1±0.6	A

[†], Extent is measured as the percentage (elsewhere in this manuscript, proportion) of 98,224 grid cells in North America with a CLIMEX stress index > 99. Values represent the least-squares mean of three projection horizons: 2020; 2050; and 2080. Values for a species within a column followed by the same letter are not significantly different at $\alpha=0.05$.

[‡], least squares standard error.

Discussion

These models suggest that the geographic extent of heat stress will increase, cold stress will decrease, and drought stress will remain constant throughout North America for all three forest pathogens. Rates of change were measured by the slopes of regression lines relating the extent of stress to time. The fact that the rates of change were the same for each species was a surprise (Table 3). These species have different biological characteristics, which are reflected partially in the differences in CLIMEX parameters among species (Table 1). The different CLIMEX parameter estimates led to substantially different forecasts of the current extent of cold stress, heat stress, and drought stress among the pathogens (Table 3). The reason for the similarity in the rate of change among pathogens for each stress remains unknown and will become the focus of future investigations.

CLIMEX parameters for these three pathogens are generally consistent with the notion that alien species have broader climatic tolerances than native species. The differences between the temperature thresholds for the onset of cold stress (TTCS) and heat stress (TTHS) and between the moisture thresholds for the onset of dry stress (SMDS) and wet stress (SMWS) provide a measure of the breadth of temperature and moisture tolerances, respectively. In general, the native *A. tsugense* begins to experience heat stress when temperatures are cooler, cold stress when temperatures are warmer, and dry stress when soils are wetter than either alien species does. Different mechanisms of wet stress for *D. septosporum* and cold stress for *P. ramorum* complicate comparisons to the other two species.

With respect to my first hypothesis, I forecast that the native pathogen *A. tsugense* will experience more direct abiotic stress in the future than either of the alien pathogens (Fig. 1). This future difference, though, stems from the substantially greater extent of abiotic stresses currently experienced by *A. tsugense* than either alien pathogen

Table 3. Regression results for the proportion of North American grid cells with CLIMEX stress indices >99 over time[†].

Stress	Species	Intercept (\pm LSSE) [‡]	Slope (\pm LSSE)	
Cold	<i>Arceuthobium tsugense</i>	0.78 \pm 0.02	A	-0.03 \pm 0.01
	<i>Dothistroma septosporum</i>	0.19 \pm 0.02	C	-0.05 \pm 0.01
	<i>Phytophthora ramorum</i>	0.35 \pm 0.02	B	-0.05 \pm 0.01
Heat	<i>Arceuthobium tsugense</i>	0.26 \pm 0.02	A	0.03 \pm 0.01
	<i>Dothistroma septosporum</i>	0.23 \pm 0.02	A	0.04 \pm 0.01
	<i>Phytophthora ramorum</i>	0.14 \pm 0.02	B	0.04 \pm 0.01
Drought	<i>Arceuthobium tsugense</i>	0.49 \pm 0.01	A	< -0.01 \pm 0.004
	<i>Dothistroma septosporum</i>	0.01 \pm 0.01	C	<0.01 \pm 0.004
	<i>Phytophthora ramorum</i>	0.14 \pm 0.01	B	< -0.01 \pm 0.004

[†], Stress indices were calculated in CLIMEX, and values > 99 indicate locations where a species is projected not to persist year-round due to that abiotic stress. Values for a stress within a column followed by the same letter are not significantly different at $\alpha = 0.05$.

[‡], least-squares standard error.

considered in this study. Future climate conditions do not disproportionately affect the rate of change in the extent of stress experienced by the native pathogen over the two alien species. Thus, I cannot conclude that climate change is creating greater areas of suitable climate for alien pathogens than for native pathogens.

My results suggest that cold stress currently is having a substantial effect on climatically suitable areas for *A. tsugense*, *D. septosporum*, and *P. ramorum* in North America. Cold stresses for *A. tsugense* and *P. ramorum* currently extend over a greater area than heat stress or drought stress (Fig. 1A, C), and for *D. septosporum*, the extent of cold stress and heat stress are effectively the same (Fig. 1B). Cold is likely to remain the most extensive abiotic stress for *A. tsugense* through 2080 (Fig. 1A) and for *P. ramorum* through approximately 2065 (Fig. 1C). For *D. septosporum*, however, cold stress will affect a smaller proportion of North America than heat stress by 2020. These results would support the value of additional research on the effects of cold temperatures on inoculum viability over time, especially for *A. tsugense* and *P. ramorum*.

With respect to the second hypothesis, I found that general circulation models differed in the extent of abiotic stress projected for each pathogen. These patterns were not always consistent among pathogens. For example, forecasts of cold stress from HadCM3 were significantly greater than from CGCM1 or CSIRO Mk2 for *A. tsugense*. For *D. septosporum* and *P. ramorum*, CSIRO Mk2-based forecasts suggested less cold stress than either of the other two general circulation models (Table 2). These results point to the value of considering multiple general circulation models when developing forecasts of where abiotic stresses might affect particular pathogens.

Climate change is likely to affect more than just the potential magnitude of abiotic stresses that act on these pathogens. Climate change may also directly affect the duration of temperature and moisture conditions that would be suitable or optimal for pathogen growth (Boland et al. 2004). Climate change may also indirectly affect the course of a plant-disease epidemic by altering the susceptibility of the host (Boland et al. 2004; Dukes et al. 2009; Hepting 1963; Sturrock et al. 2011). Trees under drought stress, for example, become more susceptible to infection by foliar pathogens than non-stressed trees (Jactel et al. 2012). Climate change may also alter the synchrony between inoculum production and the availability of sensitive plant tissues for infection (reviewed in Garrett et al. 2006). Nevertheless, the focus on direct abiotic stress that might act on forest diseases in the future is a reasonable first step. Such forecasts describe where pathogens are likely to occur year-round in the future and are useful, though imperfect, predictors of potential future impact (Boland et al. 2004).

Management decisions in agroforestry and perennial cropping systems span decades, and decisions made today rely on assumptions about future productivity and marketability of a crop. For example, the decision about which species or genetic lines to plant at a site is a management choice with ramifications potentially for the next 30 to 100 years (Pearse 1967). If trees are managed for carbon sequestration, rotations of 120 years might be optimal (Liski et al. 2001). In the past, managers might have

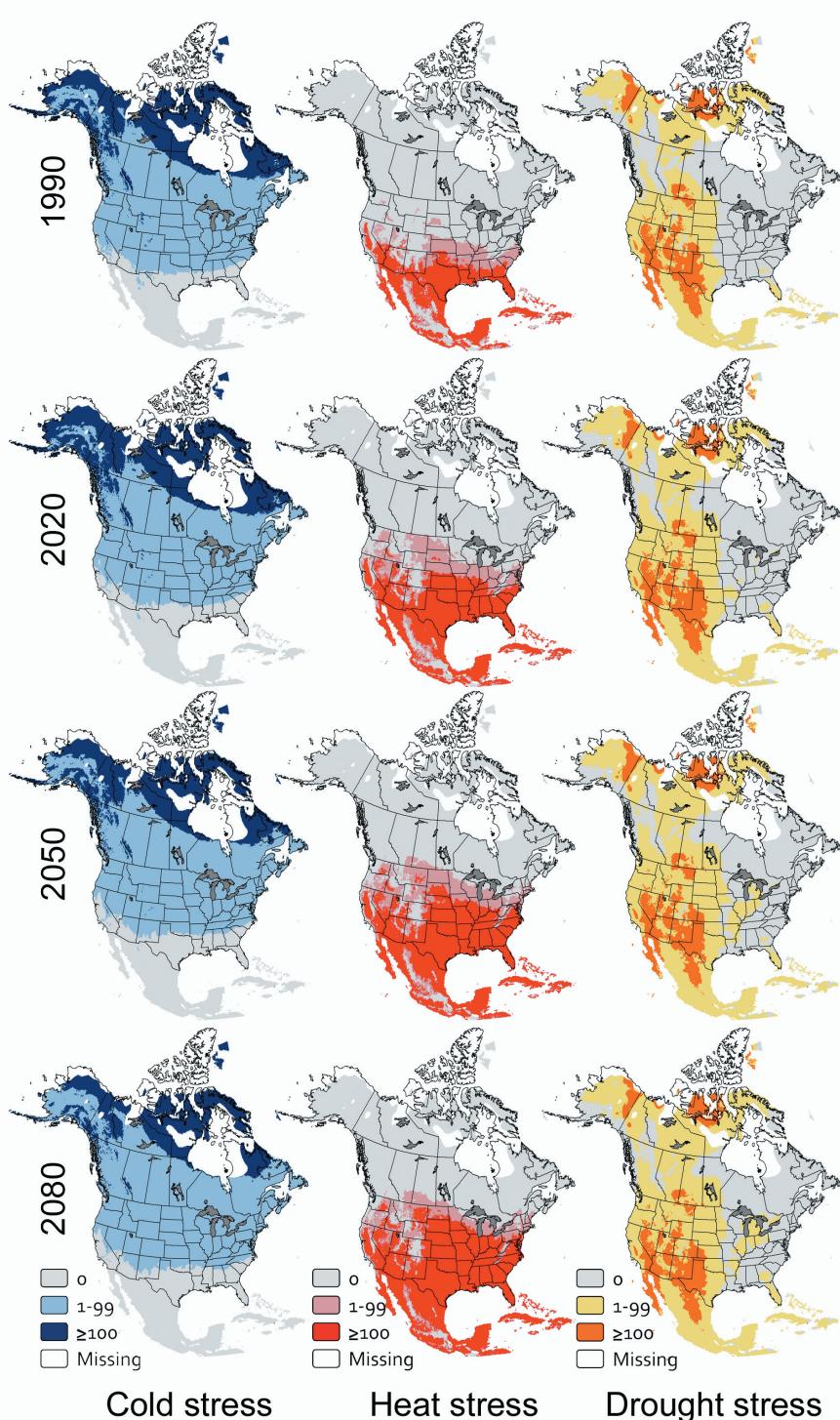


Figure 4. CLIMEX stress indices over time for *Phytophthora ramorum* in North America.

assumed that the environment would remain relatively stable over the lifetime of the crop. With this assumption, standard tree growth and mortality curves would yield suitably reliable forecasts of future harvests at different points in time (Dale et al. 1985). Minor losses of trees from pest and pathogen activity might be acceptable to some people, and outbreaks could be viewed as undesirable but not unforeseen events. Amidst growing evidence of a changing climate, managers are being encouraged to implement adaptive management strategies before the full effects of climate change manifest to improve the likelihood of meeting desired objectives (Spittlehouse and Stewart 2003). After tree planting has occurred, adaptive management options for forest health protection include removing diseased trees, thinning stands, applying pesticides, or shortening rotation length.

Pest risk maps that incorporate the effects of climate change should help land managers with longer-term planning activities and shorter-term management choices. For example, the maps developed as part of this project illustrate where abiotic stresses might exclude, or conversely might not exclude, three economically significant pathogens over time. So, these maps could be useful to decide whether trees with resistance to these pathogens should be planted, or if susceptible trees have already been planted, when to begin disease surveys. An additional benefit of these maps is that they capture complex dynamics (Figs 2–4). For example, while the total area that is at least marginal for *D. septosporum* is shrinking in North America, the area that is highly suitable is increasing (data not shown). So at a continental scale, climate change may be ameliorating some of the effects of this pathogen, but at a local or regional scale, climate change may be intensifying its effects. Qualitative characterizations of the effects of climate change are sensitive to the scales at which the assessments are made.

Forecasts of future disease activity based on climate normals will have limited utility over time. We found significant changes in abiotic stresses acting on each pathogen in each 30 yr projection horizon (Fig. 1). Our results suggest that models based on climate normals are likely to be useful for less than 30 yr.

CLIMEX focuses on abiotic drivers of population growth and death for ectothermic species. A benefit of this approach is that parameters have direct relevance to mechanisms underlying population change. Parameters estimated through inductive procedures, i.e., derived from known occurrences of a species, can suffer from some of the same limitations as other inductive species distribution models with respect to the vagaries of presence or absence records (Venette et al. 2010). But, unlike some other species distribution models, CLIMEX parameter estimates can be evaluated against extant literature on the autecology of the species or tested with appropriately designed experiments. A potential limitation of most species distribution models is that they fail to account for longer-term adaptation of a species to its environment, e.g. natural selection for drought or cold tolerance (Morey et al. 2013). More work is needed to account for additional sources of uncertainty in projections of the effects of climate change on the distribution and activity of forest pathogens and to express this uncertainty in ways that can be formally incorporated into decision-making processes.

Conclusions

Cold stress is likely to preclude the year-round establishment of *A. tsugense*, *D. septosporum*, and *P. ramorum* in many areas within North America.

With future climate change, the geographic extent of cold stress will diminish and allow for some northward movement in the range of climate suitability for these pathogens, but heat stress will increase and move southern range limits further north. Drought stress seems likely to act sporadically and not drive systematic changes the way temperature will.

The geographic extent of future cold stress, heat stress, and drought stress are forecasted to change at the same rate for the alien invasive pathogens *D. septosporum* and *P. ramorum* and the native pathogen *A. tsugense*. Future differences in the extent of abiotic stresses are the result of current differences.

The general circulation models CGCM1, CSIRO Mk2, and HadCM3 occasionally yielded different forecasts of the extent of stress for one of the three forest pathogens.

Forecasts of future pathogen occurrence or activity based on historical climate are meaningful for less than 30 yrs, less than the time horizon for many decisions in forestry.

Adaptive management strategies are needed for resource managers to remain responsive to realized future changes in the distribution and activity of forest pathogens. Pest risk maps that depict forecasts of these changes should provide useful guidance but are constrained by several sources of uncertainty.

Acknowledgements

I thank Susan Frankel for her enthusiastic support of this project and Dave Shaw, Paul Hennon, Rona Sturrock, Alex Woods, Terry Shaw, and Jim Worrall for useful conversations about these pathogens. This work was supported, in part, by funds from the Western Wildland Environmental Threat Assessment Center (USDA Forest Service, Prineville, OR). Support of the sixth annual meeting of the International Pest Risk Mapping Workgroup by OECD's Co-operative Research Programme is deeply appreciated.

References

- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259: 660–684. doi: 10.1016/j.foreco.2009.09.001

- Baker RHA, Sansford CE, Jarvis CH, Cannon RJC, MacLeod A, Walters KFA (2000) The role of climatic mapping in predicting the potential geographical distribution of non-indigenous pests under current and future climates. *Agriculture Ecosystems & Environment* 82: 57–71. doi: 10.1016/s0167-8809(00)00216-4
- Boland GJ, Melzer MS, Hopkin A, Higgins V, Nassuth A (2004) Climate change and plant diseases in Ontario. *Canadian Journal of Plant Pathology-Revue Canadienne de Phytopathologie* 26: 335–350. doi: 10.1080/07060660409507151
- Bonan GB (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* 320: 1444–1449. doi: 10.1126/science.1155121
- Canadell JG, Raupach MR (2008) Managing forests for climate change mitigation. *Science* 320: 1456–1457. doi: 10.1126/science.1155458
- Chazdon RL (2008) Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science* 320: 1458–1460. doi: 10.1126/science.1155365
- Dale VH, Doyle TW, Shugart HH (1985) A comparison of tree growth models. *Ecological Modelling* 29: 145–169. doi: 10.1016/0304-3800(85)90051-1
- Desprez-Loustau ML, Robin C, Reynaud G, Deque M, Badeau V, Piou D, Husson C, Marcais B (2007) Simulating the effects of a climate-change scenario on the geographical range and activity of forest-pathogenic fungi. *Canadian Journal of Plant Pathology-Revue Canadienne de Phytopathologie* 29: 101–120.
- Driscoll DA, Felton A, Gibbons P, Felton AM, Munro NT, Lindenmayer DB (2012) Priorities in policy and management when existing biodiversity stressors interact with climate-change. *Climatic Change* 111: 533–557. doi: 10.1007/s10584-011-0170-1
- Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? *Trends in Ecology & Evolution* 14: 135–139. doi: 10.1016/s0169-5347(98)01554-7
- Dukes JS, Pontius J, Orwig D, Garnas JR, Rodgers VL, Brazee N, Cooke B, Theoharides KA, Stange EE, Harrington R, Ehrenfeld J, Gurevitch J, Lerdau M, Stinson K, Wick R, Ayres M (2009) Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere* 39: 231–248. doi: 10.1139/x08-171
- Evans HC (1984) The genus *Mycosphaerella* and its anamorphs *Cercoseptoria*, *Dothistroma*, and *Lecanosticta* on pines. Commonwealth Agricultural Bureau, Surrey, UK.
- Farr DF, Bills GF, Chamuris GP, Rossman AY (1995) Fungi on plants and plant products in the United States. The American Phytopathological Society Press, St. Paul, Minnesota USA, 1252 pp.
- Garrett KA, Dendy SP, Frank EE, Rouse MN, Travers SE (2006) Climate change effects on plant disease: Genomes to ecosystems. *Annual Review of Phytopathology* 44: 489–509. doi: 10.1146/annurev.phyto.44.070505.143420
- Gibson IAS (1972) Dothistroma blight of *Pinus radiata*. *Annual Review of Phytopathology* 10: 51–72.
- Grunwald NJ, Garbelotto M, Goss EM, Heungens K, Prospero S (2012) Emergence of the sudden oak death pathogen *Phytophthora ramorum*. *Trends in Microbiology* 20: 131–138. doi: 10.1016/j.tim.2011.12.006

- Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* 8: 461–467. doi: 10.1111/j.1461-0248.2005.00739.x
- Hawksworth FG, Wiens D (1996) Dwarf mistletoes: biology, pathology, and systematics. US Department of Agriculture Forest Service, Washington, D.C., 410 pp.
- Hepting GH (1963) Climate and forest diseases. *Annual Review of Phytopathology* 1: 31–50.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978. doi: 10.1002/joc.1276
- Iverson LR, Prasad AM, Matthews SN, Peters M (2008) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management* 254: 390–406. doi: 10.1016/j.foreco.2007.07.023
- Ivory MH (1994) Records of foliage pathogens of Pinus species in tropical countries. *Plant Pathology* 43: 511–518. doi: 10.1111/j.1365-3059.1994.tb01585.x
- Jactel H, Petit J, Desprez-Loustau ML, Delzon S, Piou D, Battisti A, Koricheva J (2012) Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology* 18: 267–276. doi: 10.1111/j.1365-2486.2011.02512.x
- Kliejunas JT (2011) A risk assessment of climate change and the impact of forest ecosystems in the western United States and Canada. PSW-GTR-236. In: USDA Forest Service (Ed) Pacific Southwest Research Station, 70 pp.
- Liski J, Pussinen A, Pingoud K, Mäkipää R, Karjalainen T (2001) Which rotation length is favourable to carbon sequestration? *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière* 31: 2004–2013. doi: 10.1139/cjfr-31-11-2004
- McKenney DW, Pedlar JH, Rood RB, Price D (2011) Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. *Global Change Biology* 17: 2720–2730. doi: 10.1111/j.1365-2486.2011.02413.x
- Morey AC, Venette RC, Hutchison WD (2013) Could natural selection change the geographic range limits of light brown apple moth (Lepidoptera, Tortricidae) in North America? In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. *NeoBiota* 18: 151–156. doi: 10.3897/neobiota.18.5288
- Nabuurs GJ, Masera O, Andrasko K, Benitez-Ponce P, Boer R, Dutschke M, Elsiddig E, Ford-Robertson J, Frumhoff P, Karjalainen T, Krinkina O, Kurz WA, Matsumoto M, Oyhantcabal W, Ravindranath NH, SanzSanchez MJ, Zhang X (2007) Forestry. In: Metz B, Davidson OR, Bosch PR, Dave R, Meyer LA (Eds) Climate Change 2007: Mitigation Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, NY.
- Pearse PH (1967) Optimum forest rotation. *Forestry Chronicle* 43: 178–195.
- Rizzo DM, Garbelotto M, Hansen EA (2005) *Phytophthora ramorum*: Integrative research and management of an emerging pathogen in California and Oregon forests. *Annual Review of Phytopathology* 43: 309–335. doi: 10.1146/annurev.phyto.42.040803.140418
- Smith AL, Hewitt N, Klenk N, Bazely DR, Yan N, Wood S, Henriques I, MacLellan JI, Lipsig-Mumme C (2012) Effects of climate change on the distribution of invasive alien species in Canada: a knowledge synthesis of range change projections in a warming world. *Environmental Reviews* 20: 1–16. doi: 10.1139/a11-020

- Spittlehouse DL, Stewart RB (2003) Adaptation to climate change in forest management. BC Journal of Ecosystems and Management 4: 1–11.
- Sturrock RN, Frankel SJ, Brown AV, Hennon PE, Kliejunas JT, Lewis KJ, Worrall JJ, Woods AJ (2011) Climate change and forest diseases. Plant Pathology 60: 133–149. doi: 10.1111/j.1365-3059.2010.02406.x
- Sutherst RW, Maywald GF (1985) A computerized system for matching climates in ecology. Agriculture Ecosystems & Environment 13: 281–299. doi: 10.1016/0167-8809(85)90016-7
- Sutherst RW, Maywald GF, Bottomley W, Bourne A (2004) CLIMEX v2: User's guide. CSIRO, Melbourne, 100 pp.
- van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fule PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH, Veblen TT (2009) Widespread increase of tree mortality rates in the western United States. Science 323: 521–524. doi: 10.1126/science.1165000
- Venette RC, Cohen SD (2006) Potential climatic suitability for establishment of *Phytophthora ramorum* within the contiguous United States. Forest Ecology and Management 231: 18–26. doi: 10.1016/j.foreco.2006.04.036
- Venette RC, Kriticos DJ, Magarey RD, Koch FH, Baker RHA, Worner SP, Gomez Raboteaux NN, McKenney DW, Dobesberger EJ, Yemshanov D, De Barro PJ, Hutchison WD, Fowler G, Kalaris TM, Pedlar J (2010) Pest risk maps for invasive alien species: A roadmap for improvement. Bioscience 60: 349–362. doi: 10.1525/bio.2010.60.5.5
- Watt MS, Kriticos DJ, Alcaraz S, Brown AV, Leriche A (2009) The hosts and potential geographic range of Dothistroma needle blight. Forest Ecology and Management 257: 1505–1519. doi: 10.1016/j.foreco.2008.12.026
- Woods A, Coates KD, Hamann A (2005) Is an unprecedented dothistroma needle blight epidemic related to climate change? Bioscience 55: 761–769. doi: 10.1641/0006-3568(2005)055[0761:IAUDNB]2.0.CO;2

Could natural selection change the geographic range limits of light brown apple moth (Lepidoptera, Tortricidae) in North America?

Amy C. Morey¹, Robert C. Venette², William D. Hutchison¹

1 Department of Entomology, University of Minnesota, St. Paul, MN, USA **2** Northern Research Station, USDA Forest Service, St. Paul, MN 55108, USA

Corresponding author: Robert C. Venette (rvenette@fs.fed.us)

Academic editor: R. Magarey | Received 9 April 2013 | Accepted 27 May 2013 | Published 13 September 2013

Citation: Morey AC, Venette RC, Hutchison WD (2013) Could natural selection change the geographic range limits of light brown apple moth (Lepidoptera, Tortricidae) in North America? In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 151–156. doi: 10.3897/neobiota.18.5288

We artificially selected for increased freeze tolerance in the invasive light brown apple moth. Our results suggest that, by not accounting for adaptation to cold, current models of potential geographic distributions could underestimate the areas at risk of exposure to this species.

Forecasting future distributions of invasive insects is important for many management and regulatory decisions. However, numerous challenges exist in creating accurate, biologically relevant models and maps that are meaningful over time (Venette et al. 2010). In particular, no models currently account for the potential of an invasive species to adapt to a new environment. In fact, demographic models in invasion biology commonly treat species as “homogenous immutable entities” (Lee 2002). For invasions by alien species in North America, adaptation to cold temperature may be especially important at northern latitudes or high elevations; cold often prevents species from surviving year round (Huey 2010, Venette 2013). For example, cold is likely to constrain the future distribution of the light brown apple moth, *Epiphyas postvittana* (Walker), a recent insect invader to North America. No model for *E. postvittana* currently accounts for the possibility of evolution of increased cold tolerance. The objective of this study was to determine if it was possible to artificially select for increased

cold tolerance in this species, and if so, to begin exploring the subsequent geographical repercussions. *Epiphyas postvittana* is considered to be predominately freeze intolerant during its purported overwintering stage, the late instar larva (Burgi and Mills 2010), but preliminary data suggests that a small proportion of the population may also be freeze tolerant (Venette unpublished data). This phenomenon could be considered at least “partial freeze tolerance” (Sinclair 1999), and enabled freezing to act as a strong selection pressure for enhanced cold tolerance in our study.

Epiphyas postvittana eggs were obtained from USDA-APHIS (permit P526P-11-03713). All subsequent rearing and experimentation was conducted in a Biosafety Level 2 Containment Facility in St. Paul, MN. Eggs were held at 23°C, 60% RH, and resulting neonates were reared on artificial bean diet until late instars. We cooled 4–6th instars (verified through head capsule measurement; Danthanarayana 1975) individually inside gelatin capsules at ~1°C/min to their supercooling point inside a -80°C freezer (modified from Carrillo et al. 2004). Once freezing occurred, larvae were immediately returned to 23°C and given fresh diet. Mortality was measured as failure to eclose. Surviving moths were randomly mated in 0.47L (16 fluid oz) containers with 1–3 individuals of each sex. Randomly selected offspring were subsequently reared and supercooled as previously described. This procedure was repeated for nine generations. A minimum of 102 larvae were supercooled in each generation. A control population was maintained simultaneously and identically, save exposure to freezing.

Survival following freezing after nine generations was compared between the selected and control populations using non-parametric cumulative incidence functions (CIF) in SAS 9.3 (SAS Institute, Cary, N.C.) to address competing risk (Satagopan et al. 2004). The competing risk was any individual that froze and survived. These estimates were then used to calculate the temperature required to kill 50% (LT_{50}) of each population.

We used NAPPFAST (Magarey et al. 2009) to map where temperatures might fall below the LT_{50} of the selected or control populations. For each 10 × 10km grid cell, NAPPFAST calculated the proportion of the last 10 years in which the lowest temperature of the year was colder than the LT_{50} for each population. We ran the model with 3-D interpolated climate data.

After only nine generations of selection, the probability of survival following freezing was significantly ($\alpha=0.1$) greater for the selected population than the unselected control (Fig. 1; $P= 0.078$, $df=1$, $\chi^2 = 3.11$). The LT_{50} for the unselected and selected populations were estimated to be -16.5°C and -19.0°C, respectively.

Figure 2 illustrates the geographic significance of a putative increase in cold tolerance for *E. postvittana*. Dark blue areas indicate the most dramatic effect of cold, where the LT_{50} was reached in 9–10 of the 10 years modeled. Cold was sufficient to exclude *E. postvittana* in many northern areas (e.g., Minnesota, the Dakotas, Wyoming, and much of Canada) using either the unselected (Fig. 2a) or selected (Fig. 2b) model. However, for other mid-western, eastern, and southern states, there was an overall reduction in the number of years where the LT_{50} was reached when using the selected population; the light blue to dark green colors shifted north. For example, the unselected model projected that nearly all of Michigan would reach the LT_{50} during 90–100% (dark

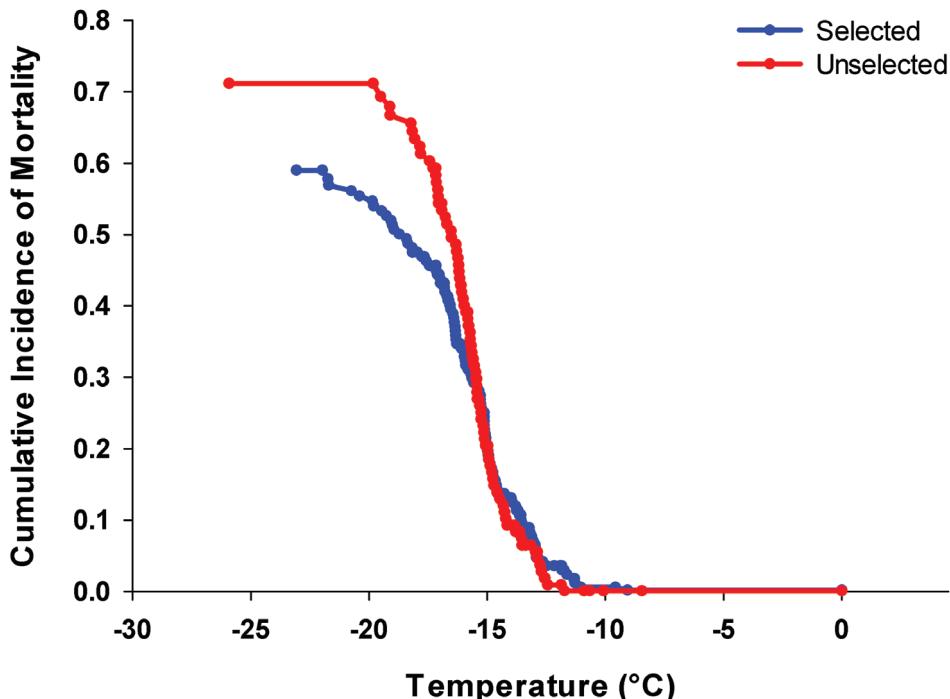


Figure 1. Cumulative incidence of mortality of *E. postvittana* late instars with (n=179) and without (n=109) nine generations of artificial selection for increased cold tolerance.

blue) of the years modeled. In contrast, the selected model projected that most of the state would only reach the threshold between 50 to 80% of the modeled years (light blue and white). Similarly, western states (e.g., Nevada and Idaho) showed an eastward shift in the number of years that temperatures did not reach the LT₅₀.

Current risk maps that exist for *E. postvittana* (e.g., Fowler et al. 2009, Gutierrez et al. 2010, Lozier and Mills 2011), acknowledge the importance of cold in shaping this species' potential U.S. range. However, the parameter(s) used to describe cold tolerance is/are assumed to be static. If natural selection follows a pattern similar to what our research suggests, within a relatively short period, current models may underestimate the risk of *E. postvittana* exposure in some areas in the future.

Uncertainty is inherent in pest risk models and contending with it is an ongoing area of research (Venette et al. 2010). Our study attempted to address the uncertainty related to the potential of a species to adapt to a cold environment and highlighted the geographic consequences if adaptation to cold is not considered. However, other sources of uncertainty still remain and are important future directions of this work. For example, the time of year may influence the effectiveness of selection on *E. postvittana*, assuming multi-voltinism and a randomly mating population. Selection is only likely to increase cold tolerance when there is a strong pressure (winter). But if there is any

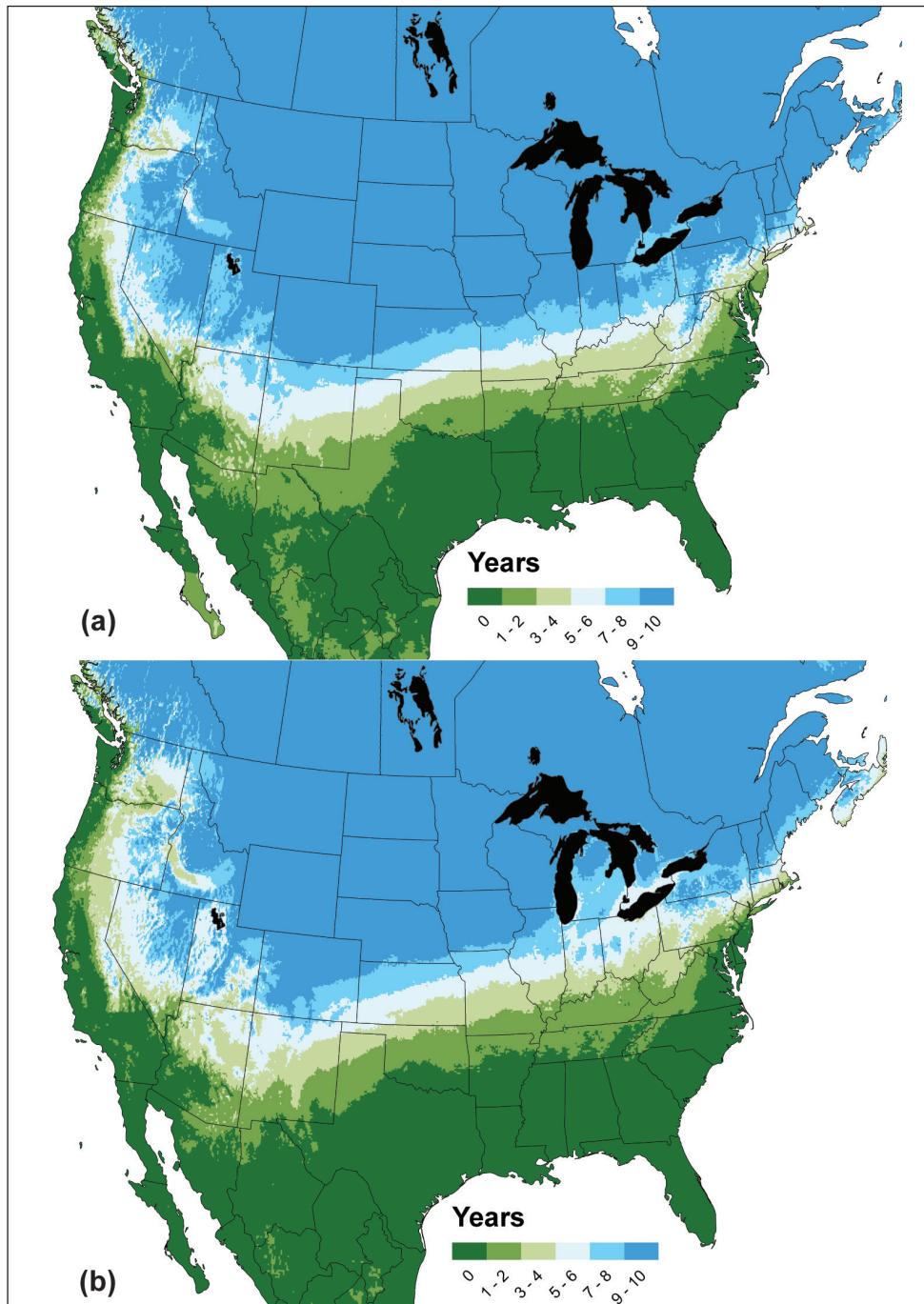


Figure 2. The frequency of years (2003–2012) in which temperatures fell below the threshold required to cause 50% mortality (LT_{50}) of *E. postvittana* in North America: **a** without selection, and **b** after nine generations of selection for increased freeze tolerance. Dark blue indicates where the LT_{50} was reached in 9–10 of the 10 years, dark green indicates where the LT_{50} was never reached during the 10-yr period.

trade-off between increased cold tolerance and fitness (see Watson and Hoffman 1996, Huey 2010), cold adapted individuals may be selected against during months when selection pressure is reduced (summer). Similarly, particularly for a highly polyphagous insect like *E. postvittana*, host plant variability could also affect cold tolerance measures (e.g., Liu et al. 2009). Understanding the relationship between cold tolerance and these additional factors will undoubtedly continue to further enhance the accuracy and ultimate utility of pest risk mapping tools.

Acknowledgements

We thank Glen Fowler, Tracy Twine, and Tim Kurtti for comments on an earlier draft. We are also grateful for the assistance of Erica Nystrom, Laurel Mosca, Alex Sloane, and Kiley Friedrich in data collection, and to the MAES/MDA BSL-2 staff. This project was supported in part by a U.S. National Science Foundation (NSF)-Integrative Graduate Education and Research Traineeship Fellowship and the USDA Forest Service. We also thank NSF-Research Coordination Networks-FORECAST for funding A.C. Morey's participation in the sixth annual meeting of the International Pest Risk Mapping Workgroup.

References

- Burgi LP, Mills NJ (2010) Cold tolerance of the overwintering larval instars of light brown apple moth *Epiphyas postvittana*. Journal of Insect Physiology 56: 1645–1650. doi: 10.1016/j.jinsphys.2010.06.009
- Carrillo MA, Kaliyan N, Cannon CA, Morey RV, Wilcke WF (2004) A simple method to adjust cooling rates for supercooling point determination. CryoLetters 25: 150–160. <http://www.ingentaconnect.com/content/cryo/cryo/2004/00000025/00000003/art00001>
- Danthanarayana W (1975) The bionomics, distribution and host range of the light brown apple moth, *Epiphyas postvittana* (Walk.) (Tortricidae). Aust. J. Zoology 23: 419–437. doi: 10.1071/ZO9750419
- Fowler G, Garrett L, Neeley A, Magarey R, Borchert D, Spears B (2009) Economic Analysis: Risk to U.S. apple, grape, orange, and pear production from the light brown apple moth, *Epiphyas postvittana* (Walker). USDAO-PHIS-PPQ-CPHST-PERAL, 28pp. http://www.aphis.usda.gov/plant_health/plant_pest_info/lba_moth/downloads/lbameconomicanalysis.pdf
- Gutierrez AP, Mills NJ, Ponti L (2010) Limits to the potential distribution of light brown apple moth in Arizona–California based on climate suitability and host plant availability. Biological Invasions 12: 3319–3331. doi: 10.1007/s10530-010-9725-8
- Huey RB (2010) Evolutionary physiology of insect thermal adaptation to cold environments. IN: Denlinger D, Lee R (Eds) Low temperature biology of insects. Cambridge Univ. Press, New York, 223–241.

- Lee CE (2002) Evolutionary genetics of invasive species. *Trends in Ecology and Evolution* 17: 386–391. doi: 10.1016/S0169-5347(02)02554-5
- Lozier JD, Mills NJ (2011) Predicting the potential invasive range of light brown apple moth (*Epiphyas postvittana*) using biologically informed and correlative species distribution models. *Biological Invasions* 13: 2409–2421. doi: 10.1007/s10530-011-0052-5
- Liu Z, Gong P, Heckel DG, Wei W, Sun J, Li D (2009) Effects of larval host plants on over-wintering physiological dynamics and survival of the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Journal of Insect Physiology* 55:1–9. doi: 10.1016/j.jinsphys.2008.07.017
- Magarey R, Borchert D, Fowler G (2009) Weather-based pest risk mapping project 2009 Final Report. Online: http://www.nappfast.org/reports/Nappfast-2009-annual-report_RMP_2_March_4_2010.pdf
- Satagopan JM, Ben-Porat L, Berwick M, Robson M, Kutler D, Auerbach AD (2004) A note on competing risks in survival data analysis. *British Journal of Cancer* 91: 1229–1235. doi: 10.1038/sj.bjc.6602102
- Sinclair BJ (1999) Insect cold tolerance: How many kinds of frozen? *European Journal of Entomology* 96: 157–164.
- Venette RC (2013) Incorporating climate change into pest risk models for forest pathogens: a role for cold stress in an era of global warming? In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. *NeoBiota* 18: 131–150. doi: 10.3897/neobiota.18.4047
- Venette RC, Kriticos DJ, Magarey RD, Koch FH, Baker RHA, Worner SP, Gomez Raboteaux NN, McKenney DW, Dobesberger EJ, Yemshanov D, De Barro PJ, Hutchison WD, Fowler G, Kalaris TM, Pedlar J (2010) Pest risk maps for invasive alien species: A roadmap for improvement. *BioScience* 60: 349–362. http://www.forestthreats.org/www/efetac4/efetac4/products/publications/Pest_risk_maps_for_invasive_alien_species.pdf/view, doi: 10.1525/bio.2010.60.5.5
- Watson MJO, Hoffmann AA (1996) Acclimation, cross-generation effects, and the response to selection for increased cold resistance in *Drosophila*. *Evolution* 50: 1182–1192. Online: <http://www.jstor.org/stable/2410659>, doi: 10.2307/2410659

Uncertainty and sensitivity analysis in quantitative pest risk assessments; practical rules for risk assessors

David Makowski¹

¹ INRA, UMR 211 INRA AgroParisTech 78850 Thiverval-Grignon France

Corresponding author: David Makowski (makowski@grignon.inra.fr)

Academic editor: Susan Worner | Received 19 September 2012 | Accepted 28 May 2013 | Published 13 September 2013

Citation: Makowski D (2013) Uncertainty and sensitivity analysis in quantitative pest risk assessments; practical rules for risk assessors. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 157–171. doi: 10.3897/neobiota.18.3993

Abstract

Quantitative models have several advantages compared to qualitative methods for pest risk assessments (PRA). Quantitative models do not require the definition of categorical ratings and can be used to compute numerical probabilities of entry and establishment, and to quantify spread and impact. These models are powerful tools, but they include several sources of uncertainty that need to be taken into account by risk assessors and communicated to decision makers. Uncertainty analysis (UA) and sensitivity analysis (SA) are useful for analyzing uncertainty in models used in PRA, and are becoming more popular. However, these techniques should be applied with caution because several factors may influence their results. In this paper, a brief overview of methods of UA and SA are given. As well, a series of practical rules are defined that can be followed by risk assessors to improve the reliability of UA and SA results. These rules are illustrated in a case study based on the infection model of Magarey et al. (2005) where the results of UA and SA are shown to be highly dependent on the assumptions made on the probability distribution of the model inputs.

Keywords

Model, Pest risk assessment, Sensitivity, Uncertainty

Introduction

Different types of mathematical models are commonly used for pest risk analysis. Some models are used for calculating probability of entry (e.g., Roberts et al. 1998). Others are used to estimate pest establishment potential (e.g., Dupin et al. 2011; Phillips et al. 2006, Roura-Pascual et al. 2009; Sutherst 2003; Webber et al. 2011; Young et al. 1999). Models are also used to model spread (e.g. Pitt et al. 2010, Robinet et al. 2012) or pest impacts under different scenarios (e.g., Stansbury et al. 2002, Cook et al. 2012; Kriticos et al. 2013). These models are powerful tools, but they include several sources of uncertainty that need to be taken into account by risk assessors and communicated to decision makers, namely uncertainty associated with input variables, parameter values estimated from expert knowledge, parameter values estimated from data, and equations, for example, uncertainty about the best equation to use for a given model application.

Uncertainty and sensitivity analysis are two techniques for evaluating models. Although both techniques are often mixed together, they each have a different purpose. Uncertainty analysis (UA) comprises a quantitative evaluation of uncertainty in model components, such as the input variables and parameters for a given situation, to determine an uncertainty distribution for each output variable rather than a single value (Monod et al. 2006; Vose 2000, de Rocquigny et al. 2008). Uncertainty in input variables and parameters is usually described using probability distributions. The objective of an uncertainty analysis is to study the consequence of uncertainty by computing a probability distribution on model output from the set of probability distributions on model inputs. UA aims to answer the following question, “what is the uncertainty associated with the output resulting from the uncertainty associated with the inputs?”

The use of formal uncertainty analysis was recently considered as one of the most important accomplishments in risk analysis since the 1980s (Greenberg et al. 2012). Uncertainty analysis allows one to take uncertainty into account when calculating an output variable of interest (e.g., number of spores entering in a given area, Peterson et al. 2009). Uncertainty analysis should be a key component of model-based risk analysis because it provides risk assessors and decision makers with information about the accuracy of model outputs.

The main purpose of sensitivity analysis (SA) is to determine how sensitive the output of a model is with respect to elements of the model subject to uncertainty. The objective of a sensitivity analysis is to rank uncertain inputs according to their influence on the output. Sensitivity analysis can be seen as an extension of uncertainty analysis. Its purpose is to answer the following question “What are the most important uncertain inputs?”. Sometimes, SA is also used for a more general purpose such as to understand how the model behaves when some input or parameter values are changed.

Uncertainty and sensitivity analysis are becoming more popular, especially due to development of Bayesian methods and of specialized software and packages (e.g., the sensitivity package of R). However, these techniques should be applied with caution because several factors may influence their results (de Rocquilly et al. 2008; Saltelli et al. 2008) such that in some cases, the validity of conclusions derived from UA or SA may be limited. In

this paper, a brief overview of methods of UA and SA are given. Then, a series of practical rules that can be followed by risk assessors to improve the reliability of UA and SA results are defined. These rules are illustrated with the infection model of Magarey et al. (2005).

Brief overview of methods for uncertainty and sensitivity analysis

For some simple models, it is possible to calculate the exact probability distribution of the model output from the probability distributions of the uncertain input variables and/or parameters. However, in most cases, it is not possible to calculate the probability distribution analytically and other methods should be used. One method is to linearise the model from its derivatives in other words the derivatives of the model output with respect to its inputs and parameters. If the uncertain factors are all assumed normally distributed, then it is possible to estimate the probability distribution of the linearised model analytically which is a normal distribution whose mean and variance are functions of the means and variances of the uncertain factors. A limitation of this method is that its application is restricted to the cases where the uncertain factors are in fact normally distributed. It is sometimes more appropriate to use other distributions, especially when the random variables are discrete or when they are bounded. Another limitation is that this method can be unreliable when the linear approximation is not accurate. For these reasons, the use of a four-step method, based on Monte Carlo simulations, adapted from de Rocquilly et al. (2008), described below is recommended.

A four-step method for uncertainty analysis

Step 1. Define probability distributions for the uncertain model inputs and parameters

The uncertainty about a quantity of interest is frequently described by defining this quantity as a random variable. Uncertainty about model parameter/input values can be described using different types of probability distributions. The uniform distribution, which gives equal weight to each value within the uncertainty range, is commonly used when the main objective is to understand model behaviour, but more flexible probability distributions are sometimes needed to represent the input and parameter uncertainty. When the model input corresponds to a discrete variable, for example, the number of imported consignments, or number of successful incursions, discrete probability distributions such as the Poisson are often appropriate (e.g., Yen et al. 2010). Among continuous distributions, the well-known Gaussian distribution is often convenient, since it requires only the specification of a mean value and a standard deviation. It is often replaced by the truncated Gaussian distribution, triangular, or by beta distributions, which give upper and lower bounds to the possible values (e.g., Peterson et al. 2009; Yen et al. 2010). When the distribution should be asymmetric, for example, when input factors are likely to be near zero, log-normal, triangular, or beta distributions offer a large range of possibilities (e.g., Peterson et al. 2009). When the

input variables and parameters are not independent, it is sometimes possible to define multidimensional probability distributions, for example, the multidimensional Gaussian distribution, with non-zero covariances. Probability distributions can be derived from expert knowledge and/or from experimental data. Frequentist statistical methods can be used to estimate standard deviations and confidence intervals reflecting uncertainty due to measurement errors and data sampling procedures. Bayesian statistics offer a variety of methods and algorithms to calculate probability distributions by combining expert knowledge and data (e.g., Makowski et al. 2010; Makowski et al. 2011).

In some cases, it is difficult to define reliable probability distributions for all uncertain model inputs, i.e., probability distributions correctly reflecting the current state of knowledge about input values based on available data and expert knowledge. In such cases, it is useful to define several probability distributions and, when possible, to run the analysis for all of them and to compare the results. This method is illustrated in the example below. When the computation time is too long or when it is not possible to run the analysis several times with different distributions, it is important to present the assumptions explicitly, and to acknowledge that the results of the analysis may have been different if other probability distributions had been defined.

Step 2. Generate values from the distributions defined at step 1

Simple random sampling is a popular method for generating a representative sample from probability distributions. This sampling strategy provides unbiased estimates of the expectation and variance of random variables. Other sampling techniques like Latin hypercube can also be used, especially when the number of variables is large. It is also possible to generate combinations of values of uncertain factors by using experimental designs, for example, complete factorial designs. The latter technique was used by the European Food Safety Authority (EFSA) (2008) to combine estimated minimum, maximum, and most likely values of several uncertain input factors. The choice of the sample size, N , is critical as the reliability of the results of the analysis depends on it. The use of a small N value may lead to inaccurate estimated mean, variance, or quantiles because all of the space defined by the uncertain inputs or parameters may not be sampled, such that the resulting approximation of the probability distribution of the model output may be inaccurate. On the other hand, the use of a very high N value will lead to a large number of model simulations that may be time consuming without adding new information. The choice of the value of N is thus a compromise between computation time and accuracy.

Step 3. Compute the model output(s) for each generated input set

Once the parameter/input values have been generated, the next step consists of running the model for each unique set of parameter/input values. For example, if N was set equal to 100, the model must be run 100 times leading to 100 values per output variable. This step may be difficult when computation of model output is time-consuming and, with some very complex models, the value of N must be set equal to a small value due to computation time constraints. This third step will be easier with more simple and less computationally intensive models.

Step 4. Describe the distributions of the model outputs

The distribution of the model output values generated at step 3 can be described and summarized in a number of ways. It is possible to present the distribution graphically using, for example, scatterplots, histograms, density plots. It is also useful to summarize the distribution of the model output values by its mean, median, standard deviation, and quantile values. All these techniques have been applied in several quantitative risk assessments (e.g., Koch et al. 2009; Peterson et al. 2009; Makowski and Mittinty 2010). When several outputs are considered, it is often useful to study the relationship between different outputs using scatterplots and correlation coefficients.

Methods of sensitivity analysis

Sensitivity analysis can be seen as an extension of uncertainty analysis. It comprises computing sensitivity indices to rank uncertain input variables or parameters according to their influence on the model output. Two types of sensitivity analysis are usually distinguished: local sensitivity analysis and global sensitivity analysis (Saltelli et al. 2000). Local SA focuses on the local impact of uncertain quantities on model outputs, and is carried out by computing partial derivatives of the output variables with respect to the inputs/parameter values. With this method, the uncertain quantities are allowed to vary within small intervals around nominal values, but these intervals are not related to the uncertainty ranges of the uncertain model inputs and parameters. Contrary to local SA, global SA considers the full domain of uncertainty of the uncertain model quantities (Saltelli et al. 2008). In global SA, the uncertain inputs and parameters are allowed to vary independently within their whole range of variation.

A sensitivity index is a measure of the influence of an uncertain quantity on a model output variable. Model inputs and parameters whose values have a strong effect on the model are characterized by high sensitivity indices. Less influential quantities are characterized by low sensitivity indices. Thus, sensitivity indices can be used to rank uncertain inputs and parameters, and identify those that deserve more accurate measurements or estimation. A large number of global SA methods are available, for example, ANOVA, correlation between input factors and model outputs, methods based on Fourier series, and methods based on Monte Carlo simulations (Saltelli et al. 2000). Sensitivity indices can be computed using statistical software (e.g., the package *sensitivity* of the statistical software R <http://cran.r-project.org/web/packages/sensitivity/index.html>) or more specialized software such as Simlab (<http://simlab.jrc.ec.europa.eu/>), @Risk, or Crystalball. @Risk and Crystalball can be used with spreadsheet software and include user-friendly interfaces. With all analyses, users will have to define the probability distributions of the uncertain input variables and parameters or, at least, their possible ranges of variation. The users will also have to define the values of some tuning parameters, as shown in the example below.

Example

In this section, we present a simple example to show how uncertainty and sensitivity analysis can be used in practice. We consider the simple generic infection model for foliar fungal plant pathogens defined by Magarey et al. (2005):

$$W = \min \left\{ W_{\max}, \frac{W_{\min}}{g(T)} \right\}$$

and

$$g(T) = \begin{cases} \frac{T_{\max} - T}{T_{\max} - T_{opt}} \left\{ \frac{T - T_{\min}}{T_{opt} - T_{\min}} \right\}^{(T_{opt} - T_{\min})/(T_{\max} - T_{opt})} & \text{if } T_{\min} \leq T \leq T_{\max} \text{ and zero otherwise} \\ 0 & \text{otherwise} \end{cases}$$

where T is the mean temperature during wetness period ($^{\circ}\text{C}$), W is the wetness duration required to achieve a critical disease intensity (5% disease severity or 20% disease incidence) at temperature T . The model output is W and it is computed as a function of the input T . T_{\min} , T_{opt} , T_{\max} are minimum, optimal, and maximum temperature for infection respectively, W_{\min} and W_{\max} are minimum and maximum possible wetness duration requirement for critical disease intensity respectively. This model was used to compute the wetness duration requirement as a function of the temperature for many species and was included in a disease forecast system (Magarey et al. 2005, 2007).

T_{\min} , T_{opt} , T_{\max} , W_{\min} and W_{\max} are five species-dependent parameters whose values were estimated from experimental data and expert knowledge for different foliar pathogens (e.g., Magarey et al. 2005; EFSA 2008). However, for some species, these parameters are uncertain due to the limited availability of data (Magarey et al. 2005), and in such cases, it is important to perform uncertainty and sensitivity analysis.

In this case study, uncertainty and sensitivity analysis techniques were applied to the model defined above for infection of citrus by the fungal pathogen *Guignardia citricarpa* Kiely. According to EFSA (2008), the parameter values are uncertain for this pathogen. The uncertainty ranges considered in this case study for these parameters are presented in Table 1. All computations were done using R (<http://cran.r-project.org>) and the code is available on request.

Three series of probability distributions were defined from Table 1:

- i. Independent uniform distributions (with lower and upper bounds set equal to the values reported in Table 1)
- ii. Independent triangular distributions (with lower and upper bounds set equal to the values reported in Table 1, and the most likely values set equal to the medians of the uncertain ranges)
- iii. Triangular distributions with positive correlation between T_{\min} and T_{opt} . Values of T_{\min} were first sampled from the triangular distribution defined in ii. Values of T_{opt} were then generated by adding values sampled from a uniform distribution (14,

Table 1. Uncertainty ranges of the five model parameters for *Guignardia citricarpa* Kiely

Parameter	Lower bound	Upper bound
T_{min} (°C)	10	15
T_{opt} (°C)	25	30
T_{max} (°C)	32	35
W_{min} (h)	12	14
W_{max} (h)	35	48

16) to the values of T_{min} . With this method, T_{opt} values were always higher than 24°C and lower than 31°C, and were correlated to T_{min} . The parameter T_{opt} does not follow a triangular distribution anymore, but the other parameters are still distributed according to the triangular distributions defined in ii.

These probability distributions were based on the same information; the lower and upper bounds defined for each model parameter in Table 1. Nonetheless, these distributions describe uncertainty in different ways; the triangular distribution gives higher weights to values located in the middle of the range, and the last distribution considers that two parameters out of five are not independent.

An uncertainty analysis was performed by generating $N=1,000$ parameter values from the three probability distributions defined above successively. Results are presented in Figures 1 (probability distribution i), 2 (probability distribution ii), and 3 (probability distribution iii). The sampled parameter values are more concentrated in the central parts of their uncertainty ranges with the independent triangular distributions (Figure 2) than with the independent uniform distributions (Figure 1). Figure 3 clearly shows that, with distribution iii, T_{min} and T_{opt} were positively correlated. The 99%, 90% 10% and 1% percentiles and mean values of the model output W reported for different temperatures show that, with all probability distributions, uncertainty about fungus wetness duration requirement is quite small if the temperature is close to 27–28 °C, but much larger for temperature below 25 or above 32 (Figures 1–3). Uncertainty about the wetness duration requirement is reduced with the triangular distribution (Figure 2) compared to the uniform (Figure 1).

A sensitivity analysis was performed using the Morris method to identify the most influential parameters of the model. The method of Morris is frequently used to quickly screen among all uncertain inputs (Saltelli et al. 2000; Monod et al. 2006; Morris 1991). The main steps of the method are:

- Define a design by combining k values of the p uncertain parameters
- Add a small incremental step Δ to one uncertain parameter z_i
- Compute an “elementary effect” defined by

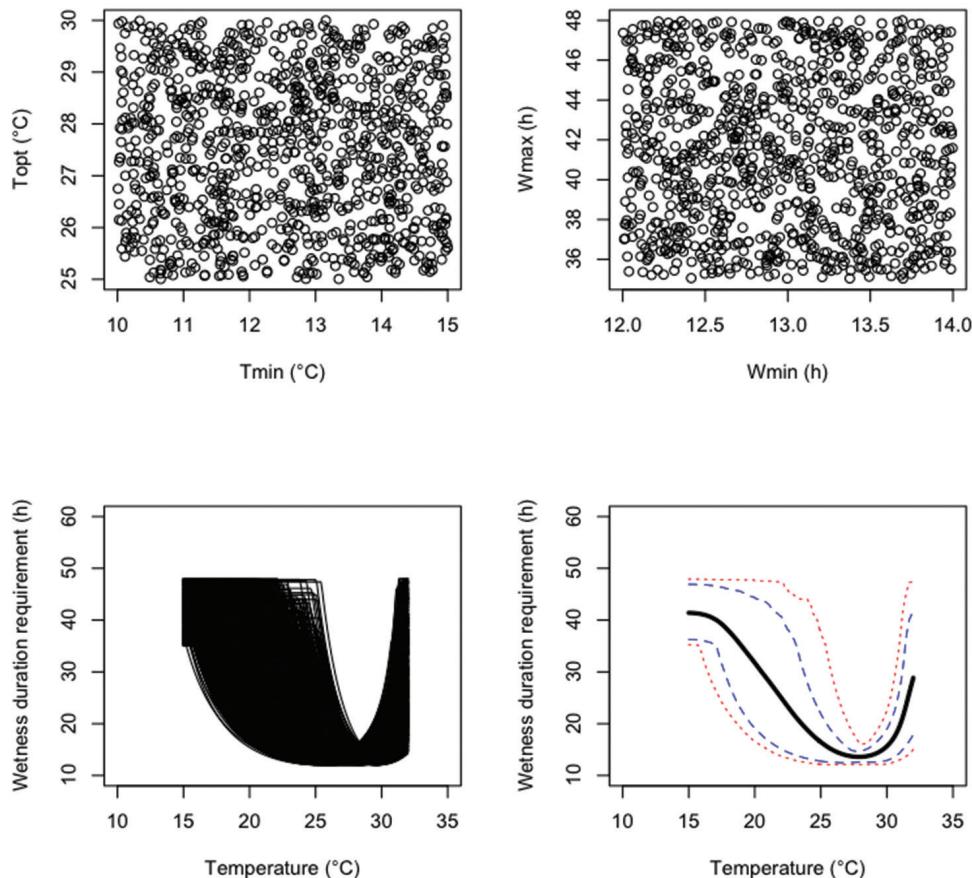


Figure 1. Results of an uncertainty analysis performed with 1,000 Monte Carlo simulations. The upper graphics show the values of four model parameters sampled from uniform distributions. The lower graphics show the resulting distribution of model outputs, their means (think black line), 10 and 90% percentiles (dashed lines), and 5 and 95% percentiles (dotted lines).

$$d_i(z) = \frac{\{y(z_1, \dots, z_{i-1}, z_i + \Delta, \dots, z_p) - y(z_1, \dots, z_p)\}}{\Delta}$$

where $y()$ is the model function and z_1, \dots, z_p are the p uncertain parameters

- Repeat the procedure several times for all uncertain parameters
- Compute the mean and variance of elementary effects from r replicates. A high mean indicates a parameter with an important influence on the output. A high variance shows that the elementary effect is highly dependent on the value of the uncertain parameter. It indicates either a parameter interacting with another parameter or indicates a parameter whose effect is non-linear. The tuning parameters of the Morris method were set equal to the following values: $k=4$, $p=5$, $\Delta=2$, and $r=100$. The lower and upper bounds of the model

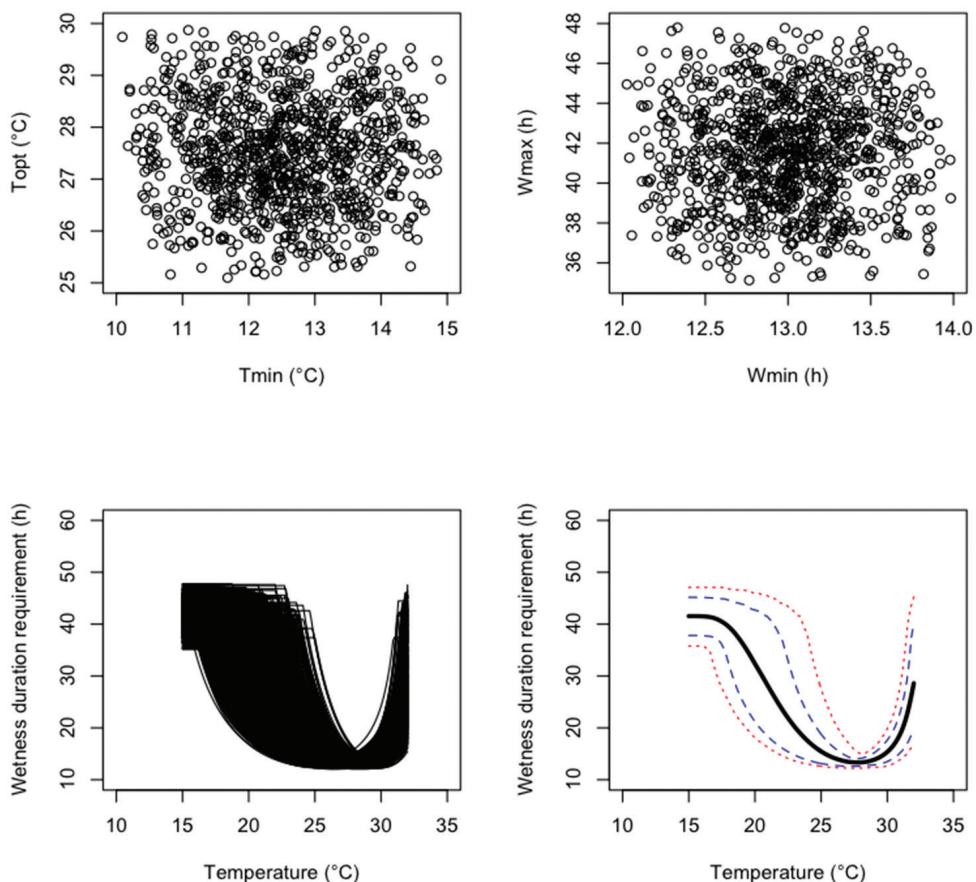


Figure 2. Results of an uncertainty analysis performed with 1,000 Monte Carlo simulations. The upper graphics show the values of four model parameters sampled from independent triangle distributions. The lower graphics show the resulting distribution of model outputs, their means (think black line), 10 and 90% percentiles (dashed lines), and 5 and 95% percentiles (dotted lines).

parameters were set equal to the values reported in Table 1. Note that it was implicitly assumed here that the uncertain model parameters were uniformly distributed.

Figure 4 shows the mean and the standard deviation of the elementary effect computed using $k=4$, $p=5$, $\Delta=2$, and $r=100$. Results show that the two most influential parameters are T_{max} and T_{opt} . The high standard deviations obtained for both parameters reveals the existence of either strong nonlinear effects or strong interactions between the two parameters. This result shows that the effects of a change of T_{max} and T_{opt} on wetness duration requirements depend on the values of these parameters (non linearity) and/or on the values of the other parameters of the model (interaction).

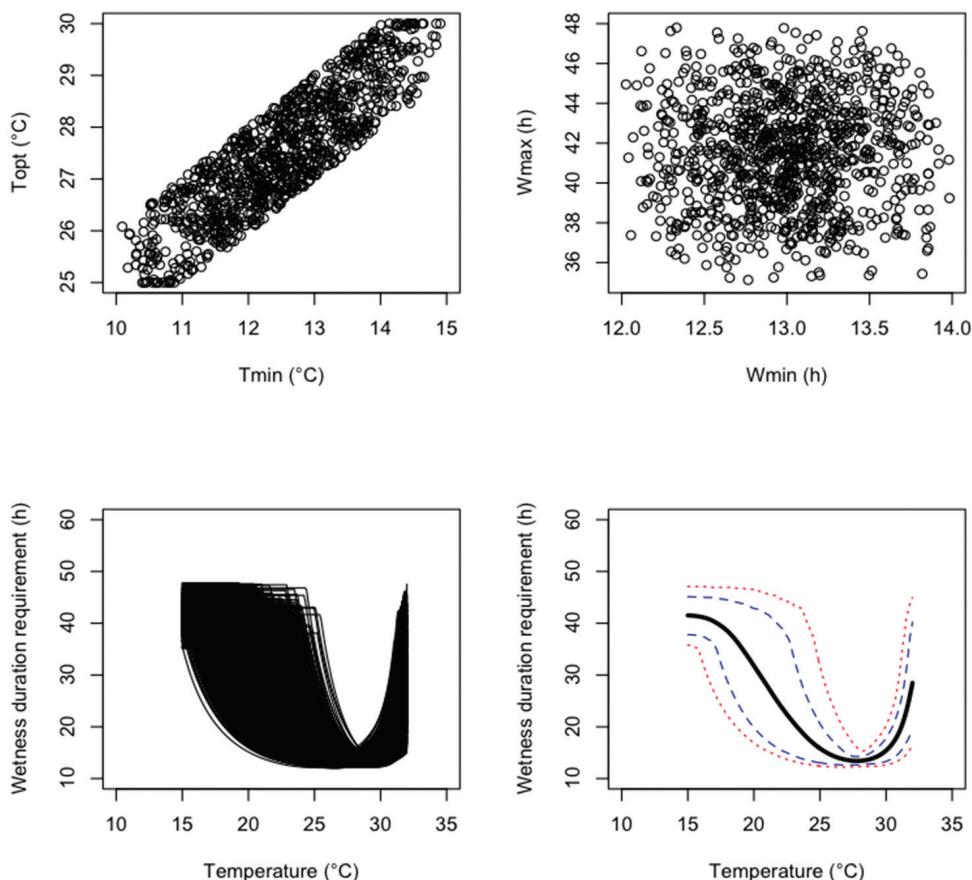


Figure 3. Results of an uncertainty analysis performed with 1,000 Monte Carlo simulations. The upper graphics show the values of four model parameters sampled from triangle distributions assuming a positive correlation between T_{min} and T_{opt} . The lower graphics show the resulting distribution of model outputs, their means (think black line), 10 and 90% percentiles (dashed lines), and 5 and 95% percentiles (dotted lines).

Practical rules

Five rules are presented below to improve the reliability of uncertainty and sensitivity analysis.

Rule 1: Be transparent about assumptions and methods

In some cases, conclusions of UA and SA depend on assumptions made on probability distributions of uncertain model inputs. Results may also depend on the selected method used to perform UA or SA. Ranking of parameters obtained by SA may thus

depend on the method used to compute sensitivity indices. For these reasons, it is important to be transparent about assumptions made on probability distributions and to present in detail the methods used for UA/SA.

Rule 2: Define precisely the model output of interest

Figures 1–3 show that the uncertainty range depends highly on the temperature T . In this example, the uncertainty level can be considered as very low or very high depending on the model output; simulated wetness duration requirements were characterized by low uncertainty levels for temperatures around 27 °C but by high uncertainty levels for more extreme temperatures. This example shows that the conclusions obtained for a given output may not be valid for others.

Rule 3: Assess the accuracy of the estimates

The accuracy of the estimated mean, variance, and quantiles of the probability distribution of the model output depends on the number of simulations. Figure 4 shows the 99%, 90%, 50%, 10%, and 1% percentiles of wetness duration requirements estimated using different numbers of simulations from 10 to 2 000 for $T=25$ °C. Estimates of the 99% percentiles of model output W were highly unstable when the number of simulations was lower than 500. In this example, at least 1 000 simulations were required to obtain accurate estimate of the 99% percentile. This result shows that it is important to check that a sufficiently high number of simulations were used in all analysis. The stability of the computed quantities can be assessed either graphically, or by computing variances, confidence intervals either analytically or by using nonparametric techniques (e.g., bootstrapping) (Saltelli et al. 2008).

Rule 4: Assess the robustness of results to distribution assumptions

Another important point to keep in mind is that results of uncertainty analysis may depend on distribution assumptions. Table 2 shows the values of the median, 95% and 99% percentiles obtained with $N=10\,000$ Monte Carlo simulations for $T=25$ °C using the three different types of probability distributions described above. The 99% percentiles obtained with the three distributions were quite different. The 99% percentile was equal to 39.61 h with independent uniform distributions, but the same percentile was lower with the two other distributions, especially with distribution ii. This example illustrates the importance of assessing the robustness of results to assumptions made on probability distributions. The first step of the uncertainty analysis method specified above (Step 1: Define probability distributions for the uncertain model inputs and parameters) is a key step, and it is important to use all available information to derive

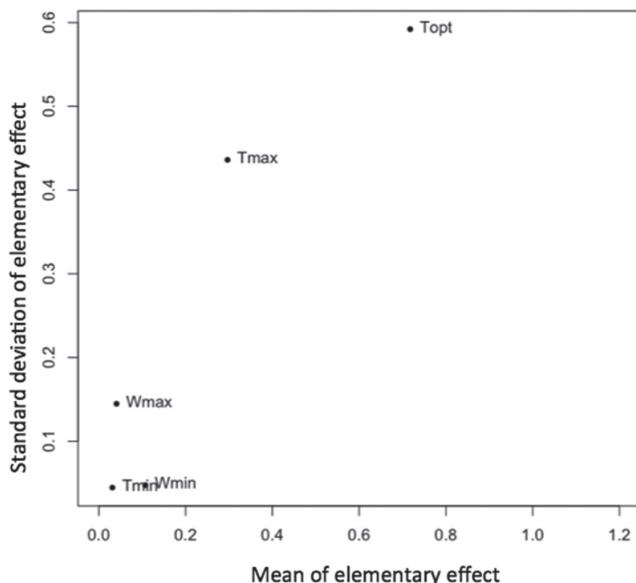


Figure 4. Results of the Morris method.

Table 2. Estimated median, 95%, and 99% percentiles of wetness duration requirements (hours) obtained under three different assumptions of probability distributions ($N=10,000$)

Prob. distribution	Median	95%	99%
i. Uniform	14.52	27.75	39.61
ii. Triangular	14.51	20.82	26.20
iii. Triangular + correlation	14.44	23.35	32.38

reliable probability distributions reflecting correctly the current state of knowledge. Although this step is often difficult, the recent development of methods of expert elicitation and of Bayesian techniques offer new possibilities (Makowski et al. 2010; Makowski et al. 2011).

Rule 5: Be aware of the capabilities of different sensitivity analysis techniques and, when possible, compare results

As mentioned above, several methods are available for uncertainty analysis and, even more, for sensitivity analysis. All methods do not have the same capabilities. For example, the Morris method illustrated in Figure 4 is an SA method that can be used to screen quickly among all uncertain inputs. However, this method cannot be used to distinguish between interaction and nonlinear effects, and other techniques for example Fourier amplitude sensitivity testing (FAST) and ANOVA should be applied when a precise analysis of interactions between model inputs is required.

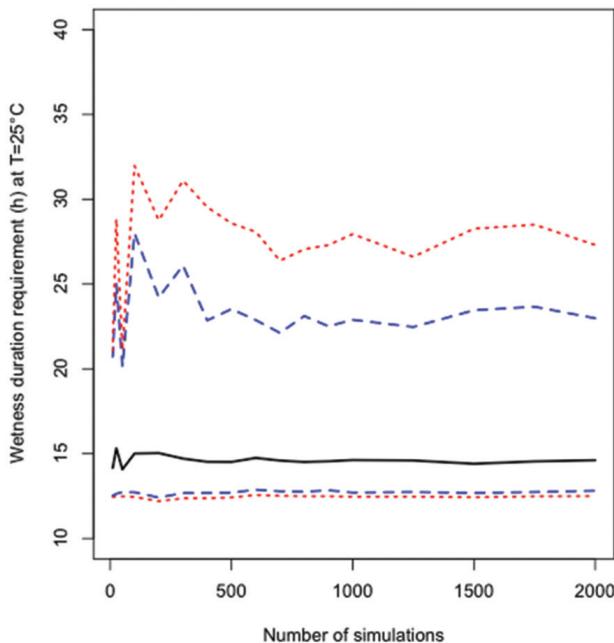


Figure 5. Estimated values of median (continuous line), 5% and 95% percentiles (dashed lines), 1% and 99% percentiles (dotted lines) of wetness duration requirements in function of the number of Monte Carlo simulations.

Conclusion

This paper shows that several factors may influence the results of uncertainty and sensitivity analysis, especially the assumptions made about the probability distributions of the uncertain model inputs and parameters, the number of simulations performed with the model, and the type of model output analyzed by the risk assessor. Due to the influence of each of these factors, the validity of the conclusions of an uncertainty or sensitivity analysis may be limited. Practical rules were presented and illustrated in this paper in order to improve the reliability of uncertainty and sensitivity analyses.

References

- Anderson RP, Lew D, Peterson AT (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecological Modelling 162: 211–232. doi: 10.1016/S0304-3800(02)00349-6
- Cook DC, Liu S, Edwards J, Villalta ON, Aurambout J-P, Kriticos DJ, Drenth A, De Barro P J (2012) Predicting the benefits of banana bunchy top virus exclusion from commercial plantations in Australia. PLoS ONE 7: e42391. doi: 10.1371/journal.pone.0042391

- de Rocquigny E, Devictor N, Tarantola S (2008) Uncertainty in industrial practice: a guide to quantitative uncertainty management. John Wiley & Sons, New York. doi: 10.1002/9780470770733
- Dupin M, Reynaud P, Jarošík V, Baker R, Brunel S, Eyre D, Pergl J, Makowski D (2011) Effects of training dataset characteristics on the performance of models for predicting the distribution of *Diabrotica virgifera virgifera*. PLoS ONE 6: 1–11. doi: 10.1371/journal.pone.0020957
- Greenberg M, Haas C, Cox A Jr, Lowrie K, McComas K, North W (2012) Ten most important accomplishments in risk analysis, 1980–2010. Risk analysis 32: 771–781. doi: 10.1111/j.1539-6924.2012.01817.x
- Koch FH, Yemshanov D, McKenney DW, Smith WD (2009) Evaluating critical uncertainty thresholds in a spatial model of forest pest invasion risk. Risk Analysis 29: 1227–1241. doi: 10.1111/j.1539-6924.2009.01251.x
- Kriticos DJ, Leriche A, Palmer D, Cook DC, Brockerhoff EG, Stephens AEA, Watt MS (2013) Linking climate suitability, spread rates and host-impact when estimating the potential costs of invasive pests. PLoS ONE 8, e54861. doi: 10.1371/journal.pone.0054861
- Magarey RD, Borchert DM, Fowler GL, Sutton TG, Colunga-Garcia M, Simpson JA (2007) NAPPFAST, an Internet System for the Weather-based Mapping of Plant Pathogens. Plant Disease 91: 336–445. doi: 10.1094/PDIS-91-4-0336
- Magarey RD, Sutton TB, Thayer CL (2005) A simple generic infection model for foliar fungal plant pathogens. Phytopathology 95: 92–100. doi: 10.1094/PHYTO-95-0092
- Makowski D, Mittinty M (2010) Comparison of scoring systems for invasive pests using ROC analysis and Monte Carlo simulations. Risk Analysis 30: 906–915. doi: 10.1111/j.1539-6924.2010.01393.x
- Makowski D, Chauvel B, Munier-Jolain N (2010) Improving weed population model using a sequential Monte Carlo method. Weed Research 50: 373–382.
- Makowski D, Bancal R, Vincent A (2011) Estimation of wetness duration requirements of foliar fungal pathogens with uncertain data. Application to *Mycosphaerella nauiae*. Phytopathology 101: 1346–1354. doi: 10.1094/PHYTO-01-11-0024
- Monod H, Naud C, Makowski D (2006) Uncertainty and sensitivity analysis for crop models. In: Wallach D, Makowski D, Jones J (Eds) Working with Dynamic Crop Models. Elsevier, 55–100.
- Morris MD (1991) Factorial sampling plans for preliminary computational experiments. Technometrics 33: 161–174. doi: 10.1080/00401706.1991.10484804
- Peterson GL, Whitaker TB, Stefanski RJ, Podleckis EV, Phillips JG, Wu JS, Martinez WH (2009) A risk assessment model for importation of United States milling wheat containing *Tilletia controversa*. Plant Disease 96: 560–573. doi: 10.1094/PDIS-93-6-0560
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231–259. doi: 10.1016/j.ecolmodel.2005.03.026
- Roberts RG, Hale CN, van der Zwet T, Miller CE, Redin SC (1998) The potential for spread of *Erwinia amylovora* and fire blight via commercial apple fruit; a critical review and risk assessment. Crop Protection 17: 19–28. doi: 10.1016/S0261-2194(98)80008-2

- Roura-Pascual N, Brotons LI, Peterson AT, Thuiller W (2009) Consensual predictions of potential distributional areas for invasive species: a case study of Argentine ants in the Iberian Peninsula. *Biological Invasions* 11: 1017–1031. doi: 10.1007/s10530-008-9313-3
- Saltelli A, Chan K, Scott M (Eds) (2000) Sensitivity Analysis. Wiley Series in Probability and Statistics. John Wiley & Sons, New York.
- Saltelli A, Ratto M, Andres T, Campolongo F, Cariboni J, Gatelli D, Saisana M, Tarantola S (2008) Global sensitivity analysis: The primer. John Wiley & Sons, New York.
- Scientific Opinion of the Panel on Plant Heath on a request from the European Commission on *Guignardia citricarpa* Kiely (2008) The EFSA Journal 925: 1–108.
- Stansbury CD, McKirdy SJ, Diggle AJ, Riley IT (2002) Modeling the risk of entry, establishment, spread, containment, and economic impact of *Tilletia indica*, the cause of karnal bunt of wheat, using an Australian context. *Phytopathology* 92: 321–331. doi: 10.1094/PHYTO.2002.92.3.321
- Sutherst RW (2003) Prediction of species geographical ranges. *Journal of Biogeography* 30: 805–816. doi: 10.1046/j.1365-2699.2003.00861.x
- Vose D (2000) Risk Analysis. 2nd edition. Wiley, Chichester.
- Webber BL, Yates CJ, Le Maitre DC, Scott JK, Kriticos DJ, Ota N, McNeill A, Le Roux JJ, Midgley GF (2011) Modelling horses for novel climate courses: insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models. *Diversity and Distributions* 17: 978–1000. doi: 10.1111/j.1472-4642.2011.00811.x
- Yen JDL, Waters EK, Hamilton AJ (2010) Cocoa pod borer (*Conopomorpha cramerella* Snellen) in Papua New Guinea: Biosecurity models for New Ireland and the Autonomous Region of Bougainville. *Risk Analysis* 30: 293–309. doi: 10.1111/j.1539-6924.2009.01297.x

Representing uncertainty in a spatial invasion model that incorporates human-mediated dispersal

Frank H. Koch¹, Denys Yemshanov², Robert A. Haack³

1 USDA Forest Service, Southern Research Station, Eastern Forest Environmental Threat Assessment Center, 3041 Cornwallis Road, Research Triangle Park, NC 27709 USA **2** Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, 1219 Queen Street East, Sault Ste. Marie, ON, P6A 2E5, Canada
3 USDA Forest Service, Northern Research Station, 1407 S. Harrison Road, East Lansing, MI 48823 USA

Corresponding author: Frank H. Koch (fhkoch@fs.fed.us)

Academic editor: S. Worner | Received 20 September 2012 | Accepted 5 March 2013 | Published 13 September 2013

Citation: Koch FH, Yemshanov D, Haack RA (2013) Representing uncertainty in a spatial invasion model that incorporates human-mediated dispersal. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 173–191. doi: 10.3897/neobiota.18.4016

Abstract

Most modes of human-mediated dispersal of invasive species are directional and vector-based. Classical spatial spread models usually depend on probabilistic dispersal kernels that emphasize distance over direction and have limited ability to depict rare but influential long-distance dispersal events. These aspects are problematic if such models are used to estimate invasion risk. Alternatively, a geographic network model may be better at estimating the typically low likelihoods associated with human-mediated dispersal events, but it should also provide a reasonable account of uncertainties that could affect perception of its risk estimates. We developed a network model that assesses the likelihood of dispersal of invasive forest pests in camper-transported firewood in North America. We built the model using data from the U.S. National Recreation Reservation Service, which document visitor travel between populated places and federal campgrounds across the U.S. and Canada. The study area is depicted as a set of coarse-resolution map units. Based on repeated simulations, the model estimates the probability that each unit is a possible origin and destination for firewood-facilitated forest pest invasions. We generated output maps that summarise, for each U.S. state and Canadian province, where (outside the state or province) a camper-transported forest pest likely originated. Treating these output maps as a set of baseline scenarios, we explored the sensitivity of these “origin risk” estimates to additive and multiplicative errors in the probabilities of pest transmission between locations, as well as random changes in the structure of the underlying travel network. We found the patterns of change in the origin risk estimates due to these alterations to be consistent across all states and provinces. This indicates that the network model behaves predictably in the presence of uncertainties, allowing future work to focus on closing knowledge gaps or more sophisticated treatments of the impact of uncertainty on model outputs.

Keywords

Human-mediated dispersal, firewood, forest pests, pest risk mapping, network modelling, uncertainty

Introduction

The spread of invasive alien species is largely facilitated by human activities such as trade and travel (Sakai et al. 2001; Horan et al. 2002; Hulme et al. 2008). Thus, reliable estimates of spread rates and patterns for these species depend upon the adequate representation of human movement in particular social and economic contexts (Keller et al. 2008; Wilson et al. 2009). Fundamentally, most modes of human-mediated dispersal are directional and vector-based, in the sense that they involve species transport by some physical agent, activity, or mechanism along defined routes connecting discrete locations (Carlton and Ruiz 2003). Classical two-dimensional spatial spread models usually depict spread as a diffusion or travelling wave process involving one or more dispersal kernels (Andow et al. 1990; Hastings 1996; Sharov and Liebhold 1998; Lewis and Pacala 2000). In these kernels, the probability of dispersal from one location to another is a function of the distance, rather than the direction, between them (Nathan 2006). Furthermore, while fat-tailed dispersal kernels (i.e., kernels where the dispersal probability declines slowly with distance) may provide more accurate depiction of long-distance dispersal, they are difficult to fit empirically because data describing long-distance dispersal events are typically rare (Nathan et al. 2003; Hastings et al. 2005). These two aspects – an emphasis on distance over direction and the challenge of adequately characterizing long-distance dispersal – are noteworthy limitations when classical spread models are subsequently used to assess invasion risks (e.g., to forecast which locations in an area of interest are most likely to be invaded within a specified time horizon).

However, there has been increased recognition of the utility of network-based modelling approaches to depict human-mediated dispersal of invasive species (Hulme 2009). Such models, which describe a species' movement via vectors, or links, between a set of interconnected nodes, have been perhaps most commonly applied for invaders of marine environments (e.g., Floerl et al. 2009), but also to depict the movement of invasive organisms through national- and global-scale commercial trade networks (Harwood et al. 2010; Kaluza et al. 2010). A key feature of the network-based approach is that the physical distance between nodes is far less important than their level of connectivity (Moslonka-Lefebvre et al. 2011); basically, the amount of movement along a vector between two nodes replaces the vector's length as the principal, or sometimes only, determinant of the likelihood of spread. By downplaying distance in favor of connectivity, network-based models may be better suited than classical spread models for depicting long-distance dispersal events (e.g., the transcontinental movement of an organism via shipped cargo), as long as the events occur within the context of the network's underlying data structure. Yet because a network model is called on to estimate the often very low likelihood values associated with long-distance events, it

is important to characterize the uncertainties associated with these estimates, since the uncertainties have some influence on their interpretation. In other words, when the estimated risk of invasion for a given location of interest is very low, it is important to understand how the estimate will behave given various uncertainties in the data and model assumptions, since they constrain the precision and thus reliability with which the estimate can be interpreted by a model user (Zeckhauser and Viscusi 1990).

In North America, there is increasing concern that forest pest invasions are being facilitated by the transport of firewood for recreational purposes (Haack et al. 2010; Tobin et al. 2010; Koch et al. 2012). The concern has been particularly motivated by the ongoing range expansion of the highly destructive emerald ash borer (*Agrilus planipennis* Fairmaire) in the eastern U.S. and Canada, as infested firewood is considered one of the insect's primary vectors of spread (Muirhead et al. 2006; Petrice and Haack 2006; Poland and McCullough 2006). Although there has been general research into the sociology behind recreational firewood usage in North America (see Jacobi et al. 2011; USDA Animal and Plant Health Inspection Service 2011), still little is known about geographic patterns of firewood movement by campers, and the implications of those patterns for invasions. In response, we developed a geographically explicit network model that assesses the likelihood of dispersal of forest pests in camper-transported firewood. We built the model using data from the U.S. National Recreation Reservation Service, which document visitor travel between the populated places where they reside and federal campgrounds across the U.S. and Canada. Among our initial objectives for this model was the ability to identify, for any location where a forest pest is believed to have been introduced via camper-transported firewood, the other location(s) from which the pest likely originated. Unfortunately, such results are not synoptic enough for broad-scale policy-making, which is rarely done at the level of individual urban areas. Therefore, we generated raster output maps that summarize, for individual U.S. states and Canadian provinces, where outside the target state or province an introduced forest pest is most likely to have originated.

Treating these output maps as a set of baseline scenarios, we explored the sensitivity of their "origin risk" estimates to errors in the probabilities of pest transmission between locations, as well as randomized removal of nodes from the underlying network. Here, we discuss the implications of these sources of uncertainty for the interpretation of the derived maps. The use of sensitivity analysis techniques to characterize the influence of uncertainty on model outputs is not unusual (Morgan and Henrion 1990; Helton and Davis 2002; Li and Wu 2006), although it remains relatively uncommon for spatially explicit analyses of invasive species risk (but see Venette and Cohen 2006; Koch et al. 2009). For this study, our primary objective was to demonstrate a simple way to identify aspects of our network model where the introduction of uncertainty provoked an inconsistent response across the set of output maps. This would allow us to determine whether any aspect of the model framework, rather than the data populating it, was a potentially problematic source of uncertainty. We view this as an essential first step in a broader analysis of uncertainty in invasive species risk maps and their underlying models.

Methods

Data source

We constructed our network model using a broad-scale data set from the U.S. National Recreation Reservation Service (NRRS), which operates an online reservation system for campgrounds and related facilities operated by the U.S. Forest Service, National Park Service, Bureau of Land Management, and other federal agencies. The available data spanned a period of greater than five years (January 2004–September 2009) and documented ~7.2 million visitor reservations, including reservations from Canada, at campgrounds and recreational facilities throughout the continental U.S. Although this is a large data set, there are many public and private campgrounds outside the NRRS system. Hence, we assumed the data to be a representative sample of all camper travel.

Each reservation record documented the visitor's origin location (i.e., by ZIP code or Canadian postal code), the destination campground, and the date of the visit. The initial processing of the NRRS data set is described in greater detail in Koch et al. (2012). Notably, the data did not indicate camper firewood usage, so our model instead depicts the general travel behaviour of all campers as documented in the data, a consistent proportion of whom we assumed were carrying potentially infested firewood (for additional discussion regarding this proportion, see Haack et al. 2010; Jacobi et al. 2011; Koch et al. 2012). We should also note that we ignored the visit date for this study, although we acknowledge that a visit's timing (e.g., in terms of a particular season) can affect the likelihood of pest emergence from firewood and subsequent establishment.

For each individual reservation, we calculated the geographic (Euclidean) distance between the visitor's origin location (i.e., the centroid of the polygon depicting the visitor's ZIP or postal code) and the destination campground. We then parsed the data into a set of unique pathway segments. Some data aggregation was necessary during this step to ensure model tractability. Conceptually, our network model is formulated as a first-order transition matrix (Karlin and Taylor 1975) that estimates the probability of travel between every possible origin-destination combination. Each reservation record in the NRRS data represented a single trip of some specified distance between a pair of origin and destination locations. Altogether, the data featured >50,000 visitor origin locations and >2500 destination locations, which translated to >973,000 pairwise combinations involving at least one visitor reservation (i.e., at least one trip) during the study period. To build a transition matrix using this many pairwise combinations was computationally impractical, so we aggregated the data at a coarse spatial resolution (into 16 × 16 km cells), ending up with a networked set of ~14,000 unique map units. These cells provided complete spatial coverage of our study area, which included both the continental U.S. and most of Canada.

Model structure

Any two map cells, designated i and j , in this networked set were connected by a unique pathway segment, ij . Each ij had a value, m_{ij} , representing the number of trips from i to j documented in the aggregated NRSS data during the study time period t (i.e., January 2004–September 2009), and another value, m_{ji} , representing the number of return trips from j back to i . We constructed a matrix, \mathbf{M} , from these m_{ij} and m_{ji} values. The size of the matrix was $n \times n$, corresponding to the number of unique map units in the aggregated data (i.e., $n = \sim 14,000$):

$$\mathbf{M} = \begin{bmatrix} 0 & m_{12} & \cdots & m_{1n} \\ m_{21} & 0 & \cdots & m_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ m_{n1} & m_{n2} & \cdots & 0 \end{bmatrix} \quad (1)$$

The non-diagonal elements of \mathbf{M} were the m_{ij} and m_{ji} values for the pathway segments connecting each (i, j) pair of map cells. The diagonal elements of \mathbf{M} , where $i = j$, were set to 0.

Based on \mathbf{M} , we constructed a probability matrix, \mathbf{P}_t , of camper travel (and by extension, transport of potentially infested firewood) along the pathway segments during the study period t . We assumed that the probability, p_{ij} , of travel along any given segment ij was linearly related to the number of trips from i to j during period t :

$$p_{ij} = m_{ij}\lambda_t \quad (2)$$

where λ_t is a scaling parameter. Ideally, the parameter λ_t would define the total likelihood (i.e., over the study period t) of camper transport of pest-infested firewood from i to j in the pathway matrix. In fact, a precise value of λ_t would be necessary to estimate an exact probability of a pest being moved from location i to j . Our objective, however, was not to derive exactly estimated output probabilities, but the more conservative goal of testing the relative sensitivity of model outputs to changes in the inputs, such that the output probabilities simply serve as a relative measure of risk. For this purpose, we only needed λ_t to be sufficiently small to ensure that the sum of the p_{ij} probabilities in each \mathbf{P}_t matrix row was below 1.

Each row of \mathbf{P}_t included another variable, $p_{i\text{term}}$, representing the probability that no camper travel (i.e., to any j) would originate at i :

$$p_{i\text{term}} = 1 - \sum_{j=1}^n p_{ij} \quad (3)$$

If $p_{i term}$ was equal to 1 for any row, then the map cell i associated with that row did not serve as a point of origin in the model. This did not preclude the cell from serving as a potential destination j . The probability matrix \mathbf{P}_t of camper travel along each pathway segment (i.e., during period t) was thus specified as follows:

$$\mathbf{P}_t = \lambda_t \mathbf{M} = \begin{bmatrix} 0 & p_{12} & \cdots & p_{1n} & p_{1term} \\ p_{21} & 0 & \cdots & p_{2n} & p_{2term} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ p_{n1} & p_{n2} & \cdots & 0 & p_{nterm} \end{bmatrix} \quad (4)$$

We used \mathbf{P}_t as the basis for 2×10^6 stochastic pathway simulations of camper travel from each cell i to other map cells. Setting i as the origin location, the model extracted the vector of travel probabilities associated with i (i.e., the probabilities in row i) from \mathbf{P}_t in order to simulate subsequent camper travel from i through the pathway network to other map cells. Briefly, in each simulation run for a given cell i , the model performed a uniform random draw against the associated row of probabilities in \mathbf{P}_t in order to select the next map cell defining the path of an individual trip. The simulation of this path continued until reaching a final destination map cell (i.e., a cell with no outgoing travel), or instead, when a terminal state (i.e., no further travel) was selected based on the $p_{i term}$ value. Regardless of the number of individual segments comprising a simulated path, we assumed that the path was completely traversed within the study period t . Consequently, for a given pathway segment ij , the probability of camper travel from location i to location j during period t was estimated as follows:

$$\varphi_{ij} = M_{ij}/M, \quad (5)$$

where M_{ij} is the number of times pathway travel from location i to j was simulated to occur, and M is the total number of simulations ($M = 2 \times 10^6$ in this study).

Out-of-state origin risk maps

The network model permitted us to generate maps where each individual cell in the study area could be set as the origin or destination location of interest. While cell-specific maps might have value when addressing specific invasion scenarios (e.g., identifying the probable source locations for a single cell found to be invaded), they do not provide a comprehensive picture of invasion risk for use in setting management priorities. So, we chose to summarize the model results in a broader context. In a previous analysis of the NRRS data (Koch et al. 2012), we found that the majority (~53%) of camping trips involved travel distances of less than 100 km. However, we also found that 10% of trips involved distances of greater than 500 km. This is consistent with other research (Haack et al. 2010; Jacobi et al. 2011; USDA Animal and Plant Health Inspection Service 2011)

suggesting that campers frequently transport firewood across state or provincial borders. Furthermore, much of the regulatory decision-making with respect to invasive species, including the implementation of firewood restrictions to limit forest pest spread, happens at the state or provincial level (Filbey et al. 2002). For these reasons, we opted to develop model outputs that characterized those locations (i.e., map cells) outside a state or province of interest that were most strongly linked to locations inside the state or province.

For each U.S. state and Canadian province, we generated a map where, for each cell i outside the target state (province), we summed the model-derived travel probabilities (i.e., the φ_{ij} values) for all pathways between i and any destination cell j within the target state (province). Essentially, each map depicts the most likely external source locations if a firewood-transported forest pest were to be discovered within the state (province) of interest. (Note that for the Canadian provinces, we assume that campers returning from U.S. locations may be transporting forest pests, despite border biosecurity measures.) A principal feature of these maps is that they highlight key “bottleneck” locations where surveillance, awareness campaigns, or quarantine procedures have the best potential to be cost-effective in terms of protecting the state (province) of interest from invasion (Hauser and McCarthy 2009). These maps served as a set of baseline maps that we could then compare to the maps generated for a set of sensitivity scenarios, described below.

Sensitivity analyses

We performed sensitivity analyses to evaluate how uncertainty in key aspects of the network model’s structure would influence the φ_{ij} probabilities estimated in the baseline maps. The primary goal of these analyses was to assess whether uncertainties in any of the tested model aspects yielded a set of output maps with spatial patterns that departed in unexpected ways from the patterns depicted in the corresponding baseline maps. We adopted a Monte Carlo simulation approach (Morgan and Henrion 1990; Crosetto and Tarantola 2001; Li and Wu 2006) for the analyses, involving three basic steps: random sampling from an input distribution defined for each aspect of interest; repeated model runs using the randomly sampled values; and summarization of these results for comparison to the baseline maps.

We focused on three model aspects for this study. Our first sensitivity scenario tested the impact of uncertainty in the network configuration by randomly removing up to 30% of nodes (i.e., map cells and their associated vectors of p_{ij} probabilities) from the network prior to each new model run. Our second sensitivity scenario tested the impact of uncertainty in the scaling parameter λ_t (see Eq. 2). In this case, we added uniform random error within the range ± 0.15 to λ_t prior to completing each new model run. Our final sensitivity scenario evaluated the impact of uncertainty in the p_{ij} values comprising \mathbf{P}_t . To test this aspect, we added uniform random error of up to 0.01 to the p_{ij} values before each new model run. Ideally, we would have repeated the three scenarios with series of bounding values. However, because of the computational complexity of this exercise, we chose a single bounding value for each sensitivity scenario

that, based on preliminary work with the model, we were confident would provide meaningful contrast to the baseline scenario.

We completed 2×10^6 pathway simulations for each sensitivity scenario. This process yielded scenario-specific maps of the φ_{ij} probabilities (see Eq. 5) for each state and province that we could compare to the corresponding baseline maps. For this comparison, we calculated and mapped the differences, in percentage terms, between the output probabilities under the baseline scenario and under each sensitivity scenario. We also calculated a Moran's I (Moran 1950) value for each difference map. Moran's I is a measure of the global (i.e., map-wide) spatial autocorrelation of values in a spatially referenced data set (Getis and Ord 1992; Perry et al. 2002). It ranges in value from -1 to 1, with values close to -1 indicating a high degree of dispersion in the data (e.g., a checkerboard spatial pattern), values close to 1 indicating a high degree of clustering, and values near 0 indicating a random spatial pattern.

We employed a simple rank-difference approach for further comparison of the baseline results to those from our third sensitivity scenario dealing with uncertainty in the p_{ij} values. After calculating the per-cell differences between the baseline and sensitivity maps for each state and province, we converted both the baseline probabilities and the calculated differences into ranks. Each cell in a given map was assigned a rank from 1 to 6 based on a global percentile distribution of the values that occurred in the maps for all states and provinces; cell values that fell within the bottom 25% of this global distribution received a rank of 1, cells in the 25–75% range received a rank of 2, cells in the 75–90% range received a rank of 3, cells in the 90–95% range received a rank of 4, cells in the 95–99% range received a rank of 5, and cells in the top 1% of this distribution received a rank of 6. We ranked each cell twice in this fashion, first according to its percentile value under the baseline scenario, then according to its percentile value in the global distribution of differences under this sensitivity scenario. Next, we calculated the change in rank between the two, which yielded an index value ranging from -5 to 5. Finally, we mapped the index values for each state and province in order to identify any spatial trends.

Results

Baseline scenario

Across all individual state and province maps created for the baseline scenario, we saw three general spatial patterns of out-of-state (or out-of-province) origin risk. First, as illustrated by the state of Alabama (Fig. 1a), there were cases where the highest origin probabilities (i.e., the per-cell φ_{ij} values) were primarily limited to a narrow fringe zone surrounding the target state. This pattern was common among states in the southeastern and northeastern U.S. The second general pattern, exemplified by Missouri (Fig. 1b), similarly featured a localized zone of high probabilities around the target state, but this was augmented by several high-probability hotspots associated with major urban areas located outside this zone. For instance, the map for Missouri

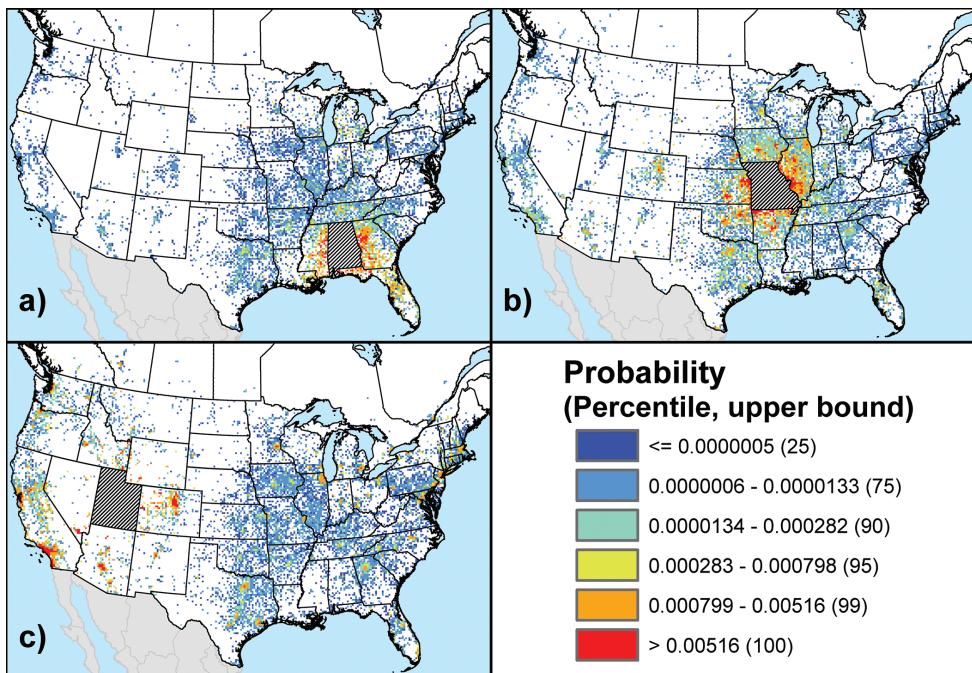


Figure 1. Out-of-state origin risk maps for three U.S. states under the baseline scenario: **a** Alabama **b** Missouri **c** Utah. The maps show the relative probability, φ_{ij} , that a map cell outside the state of interest is a source of campers carrying potentially infested firewood to the target state. Numbers in parentheses link the defined probability classes to a global percentile distribution built from the probabilities that occurred in the maps for all states and provinces.

included hotspots associated with the cities of Chicago (IL), Dallas (TX), Denver (CO), all of which are at least 400 km away. This mixed origin pattern was typical of many states in the U.S. Midwest. In the third pattern, exemplified by Utah (Fig. 1c), there was also a subtle local fringe zone, but the majority of map cells with high probabilities were associated with major urban areas that are fairly distant from the target state. With respect to Utah, the most prominent urban areas (i.e., those displaying uniformly high probabilities) were generally in the western U.S., but a number of eastern U.S. cities also had probabilities in the top 5% of the global distribution of probabilities across all states and provinces. This sort of dispersed pattern of origin risk was exhibited by other states such as Arizona and California that, like Utah, feature several popular recreational destinations (e.g., national parks) that draw campers from throughout the continent.

The maps for the Canadian provinces, especially the more populous ones (i.e., Quebec, Ontario, Alberta, and British Columbia), usually exhibited a dispersed spatial pattern similar to that observed for Utah, although the origin probabilities in each map were low compared to their U.S. counterparts. Indeed, the highest probabilities in these maps very rarely reached the top 10% of the global distribution. The only exceptions were a few high-probability (top 5%) cells in each of the maps for the most popu-

lous Canadian provinces, which appeared to be associated with specific recreational destinations such as Grand Canyon National Park (AZ) and Zion National Park (UT).

Two factors seem to govern the observed patterns of origin risk. Foremost is the population of the state or province of interest. Because the model is bi-directional (i.e., it also simulates return travel by campers from their destinations to their origin locations), the population of the target state or province influences the range of output probabilities that will be portrayed in its map, particularly the frequency at which high probabilities occur. In short, the maps of heavily populated states and provinces tended to have higher probabilities overall than sparsely populated states and provinces. The second factor is the nature of the recreational opportunities available in the target state or province. States or provinces containing several high-profile recreational destinations displayed a dispersed pattern of origin risk, while states or provinces with numerous but comparatively low-profile recreational destinations usually displayed a more localized origin risk pattern.

Impact of uncertainty in the network configuration

Figure 2 shows three example maps of the mean percent difference (i.e., over all model runs) in the φ_{ij} output probabilities under this sensitivity scenario. The example states

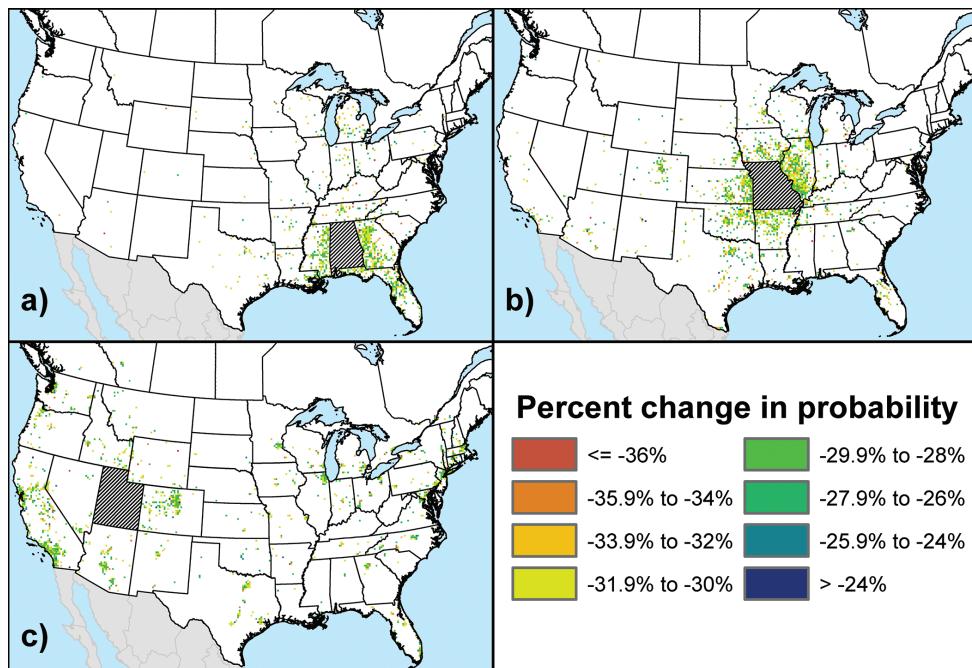


Figure 2. Maps of the mean percent difference (i.e., across all model runs) between the φ_{ij} output probabilities calculated under the baseline scenario and under the sensitivity scenario that tested the impact of uncertainty in the network configuration: **a** Alabama **b** Missouri **c** Utah. Only cells with probabilities in the top 10% of the global distribution for the baseline scenario are shown.

correspond to those highlighted under the baseline scenario: Alabama (Fig. 2a), Missouri (Fig. 2b), and Utah (Fig. 2c). Note that only map cells in the top 10% of probabilities under the baseline scenario are shown. For all states and provinces, the percent change in the values of cells in this top 10% typically ranged from -24% to -36%, with a map-wide mean (i.e., across all cells in a given map) near -30%. This level of difference is consistent with the proportion of nodes removed for this scenario. More importantly, as illustrated by the difference maps for all three example states, there was no obvious spatial trend in the pattern of change. Essentially, each map has a salt-and-pepper appearance, such that cells with higher probabilities under the baseline scenario (see Fig. 1) do not appear to have greater (or smaller) percent changes than cells with lower probabilities under the baseline. This observation is supported by the Moran's *I* values calculated for all states and provinces, which ranged between -0.016 and 0.021 (median = 0.005) and thus indicated a minimal level of spatial autocorrelation.

Impact of uncertainty in the scaling parameter λ_i

Figure 3 shows three example maps of the mean percent difference in the φ_{ij} output probabilities under this sensitivity scenario. As in the previous scenario, the example

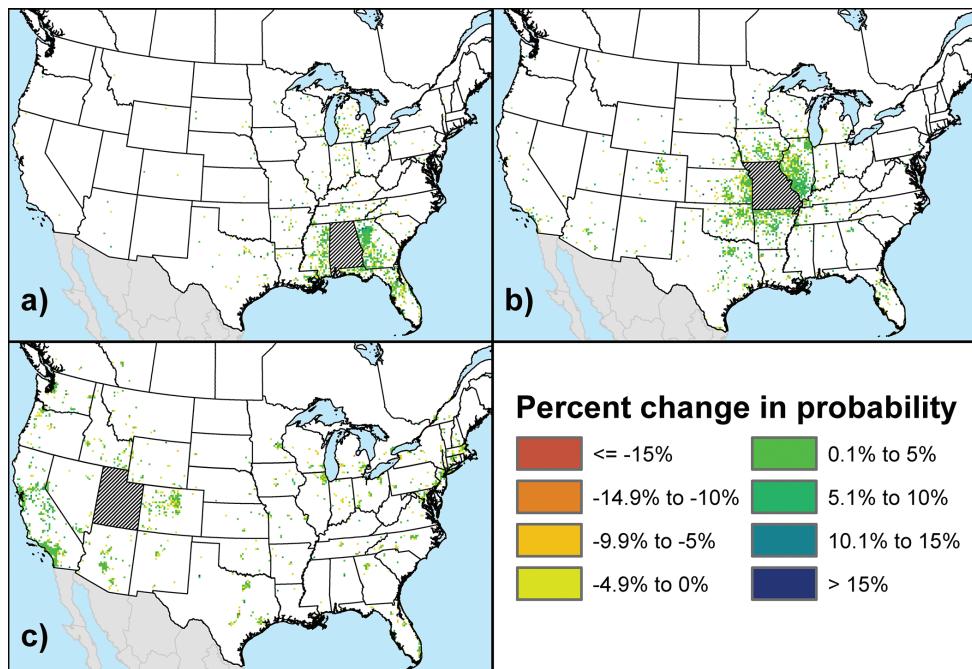


Figure 3. Maps of the mean percent difference (i.e., across all model runs) between the φ_{ij} output probabilities calculated under the baseline scenario and under the sensitivity scenario that tested the impact of uncertainty in the scaling parameter λ_i : **a** Alabama **b** Missouri **c** Utah. Only cells with probabilities in the top 10% of the global distribution for the baseline scenario are shown.

states correspond to those highlighted under the baseline scenario: Alabama (Fig. 3a), Missouri (Fig. 3b), and Utah (Fig. 3c). Only map cells in the top 10% of probabilities under the baseline scenario are shown. For all states and provinces, the percent change in the values of cells in this top 10% typically ranged from -15% to 15%, with a map-wide mean slightly greater than 0. This degree of change is consistent with the alterations to λ_i under this scenario.

None of the difference maps for the example states appears to show a strong spatial trend in the pattern of change. There may be a slight tendency for map cells with higher probabilities under the baseline scenario to exhibit small but positive percent changes, while cells with lower probabilities under the baseline may tend toward small negative changes. However, the existence of a subtle spatial trend is not really supported by the Moran's I values for each state and province, which ranged from -0.005 to 0.133 (median=0.008). Indeed, with the exception of a single Canadian province, Nova Scotia, which has relatively few connections to outside locations in our network model, none of the maps had an I value greater than 0.0324. Similar to the previous sensitivity scenario, this suggests a low level of spatial autocorrelation.

Impact of uncertainty in the p_{ij} probabilities

Figure 4 shows three example maps of the rank differences (see Methods) between the baseline scenario and this sensitivity scenario, which tested the effects of adding uniform random error to the p_{ij} probabilities. The maps display an obvious spatial trend in the pattern of change. (Again, only cells in the top 10% of probabilities under the baseline scenario are shown.) This trend can be summarized in general terms: cells with comparatively higher probabilities under the baseline scenario were more likely to exhibit a decrease or no change in rank under this sensitivity scenario, while cells with comparatively lower probabilities under the baseline were more likely to exhibit an increase in rank. Thus, for states and provinces like Alabama (Fig. 4a), where the highest origin probabilities under the baseline scenario were primarily limited to a localized zone adjoining the state or province (also see Fig. 1a), any decreases in rank were also usually limited to this zone. Alternatively, in states and provinces like Missouri (Fig. 4b) and Utah (Fig. 4c), where high origin probabilities under the baseline were regularly associated with major urban areas outside the fringe zone, it is primarily map cells in these areas that exhibited a decrease or, just as commonly, no change in rank. For all states and provinces, the map cells that exhibited increases in rank under this sensitivity scenario were usually found in rural areas or the peri-urban zones (Allen 2003) that surround large cities.

The existence of a spatial trend in the pattern of change is supported by the Moran's I values calculated for the difference maps of each state and province. With the exception of Nova Scotia, the values ranged from 0.057 to 0.208 (median = 0.135), indicating a degree of positive spatial autocorrelation (i.e., clustering) that varied according to whether the state or province of interest had a well-defined fringe zone of

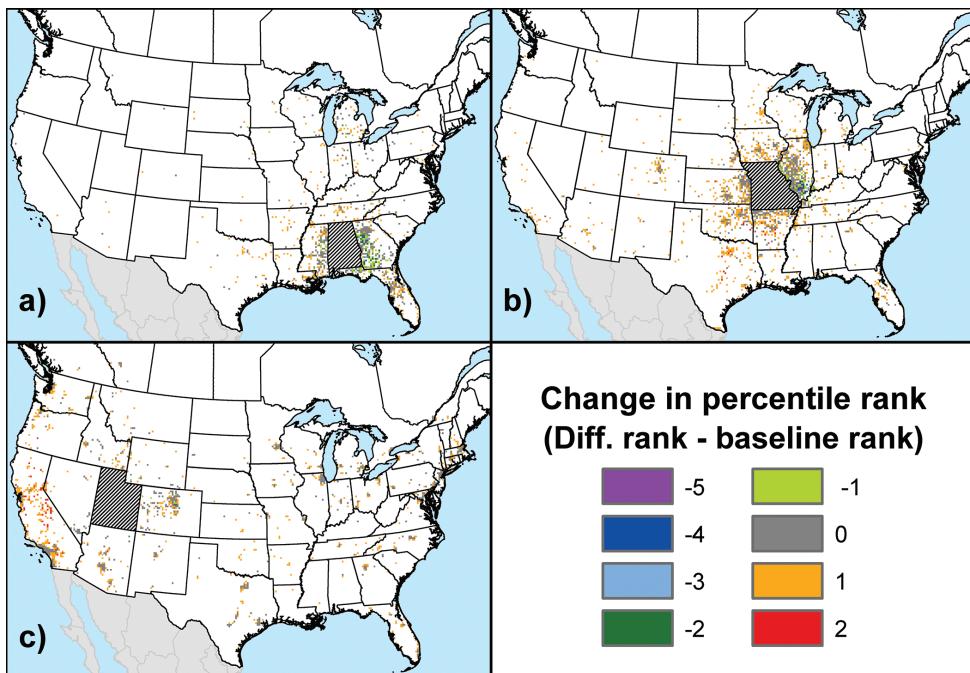


Figure 4. Maps showing the difference in rank between maps generated under the baseline scenario and under the sensitivity scenario that tested the impact of uncertainty in the p_{ij} probabilities: **a** Alabama **b** Missouri **c** Utah. See main text for details regarding the calculation of ranks, which ranged from 1 to 6 for each scenario. Only cells with probabilities in the top 10% of the global distribution for the baseline scenario are shown.

high probabilities under the baseline scenario. Typically, states and provinces with such a zone exhibited larger I values. This variability, however, does not contradict the notion of a generally consistent spatial trend across all states and provinces.

Discussion

By focusing on changes in the φ_{ij} probabilities under the sensitivity scenarios, we can make conclusions about how the model generally behaves given uncertainty in the tested model aspects. We expected to see departures from the baseline φ_{ij} values in all three scenarios, but importantly, our results indicated that the patterns of these differences were consistent across all states and provinces. In the two scenarios testing the impact of uncertainty in the network configuration and in the scaling parameter λ_p , the distribution of the mapped differences was usually close to random; in other words, no particular state (province) or range of output probabilities was uniquely affected by uncertainty in these model aspects. In the scenario that tested the impact of uncertainty in the p_{ij} values, there was a recognizable spatial trend in the differences from the baseline scenario, but this trend was manifested similarly across all states and

provinces. Essentially, uncertainty in the p_{ij} values resulted in smoothing of the φ_{ij} output probabilities across the entire map area, regardless of how those probabilities were spatially distributed under the baseline scenario.

In summary, it appears that the network model is generally stable in the presence of uncertainties in its critical structural aspects (i.e., in its spatial configuration and in parameters that define \mathbf{P}_r , the probability matrix that drives the pathway simulations). While making this determination was the primary objective of our study, close examination of the individual sensitivity scenarios reveals additional details about potential model improvements and future applications. First, removing a large portion of the nodes from the network did not cause the model to behave inconsistently. This stability suggests that the modelling framework may be transferable to other data sets that can be organized as networks, including potentially sparser data sets. This transferability may present an easy opportunity to examine other modes of human-mediated dispersal that are relevant to invasion risk. For instance, we might want to apply the model to describe camper travel patterns associated with privately owned campgrounds across North America. The framework may also be applicable to the movement of crop pests via domestic shipments of certain agricultural commodities. Similarly, the network model continued to behave consistently despite sizeable alterations to the scaling parameter λ_r . This appears to affirm our supposition that a more precise value for λ_r would not substantially affect the general behaviour of the model, which further supports the notion of its transferability to other invasion risk modelling problems.

In the sensitivity scenario that tested the impact of uncertainty in the p_{ij} probabilities, the smoothing effect observed in the output maps suggests that these probabilities were fairly sensitive to uncertainty, or at least more sensitive than the other tested model aspects. Under this scenario, a small random variate was added to every p_{ij} value in the \mathbf{P}_r matrix, including where $p_{ij} = 0$. This change effectively created new interconnecting vectors between network nodes, subsequently adding topological information to the network. Indirectly, this raised the relative importance of map cells with low origin probabilities under the baseline scenario, since it added some small probability of camper travel between cells, even in cases where no such travel was documented in the NRSS data.

Conceptually, this sensitivity scenario depicts a general lack of knowledge about the travel patterns of campers (and by extension, their movement of potentially infested firewood). This implies that the best opportunity to improve our model may be to refine the p_{ij} probabilities. Notably, these values are partly shaped by the parameter λ_r (see Eq. 2), so the issues mentioned previously regarding λ_r may have relevance here. Indeed, while we did not implement a sensitivity scenario where λ_r and the p_{ij} values were varied together, it is possible that the p_{ij} values are more or less sensitive depending on the value of λ_r . This is a potential topic of future work. Regardless, the p_{ij} values are directly derived from the data underlying the network, and so depend on the comprehensiveness and representativeness of those data for the phenomenon being modelled. In our case, the NRSS data only cover a limited subset of all camper travel, so there could be some advantage to including other data sources such as camper res-

ervation records at private- or state/provincial-managed campgrounds, contingent on the availability of such data.

We must reiterate that the φ_{ij} output probabilities only provide a relative measure of invasion risk. Because we did not have sufficient data to directly model the movement of forest pests in infested firewood, and instead modelled the travel of all campers as a proxy, then the resulting probabilities should not be interpreted as a depiction of the true risk. The actual probabilities of successful forest pest introduction via firewood are likely much lower than the numbers we present here, for various reasons; for instance, not all campers transport firewood, not all of the firewood they transport is infested, and not all infested firewood contains enough individuals of a potential pest species to support establishment upon arriving at a destination (Haack et al. 2010; Haack et al. 2011; Jacobi et al. 2011; Koch et al. 2012). Being able to better define λ_t might bring us closer to estimating the true probabilities. However, it may be worth considering whether this would be a cost-effective expenditure of research effort. For example, developing a continuous function relating travel distance to the likelihood a camper is transporting firewood might require extensive surveys of camper behaviour, and then would only provide a partial estimate of λ_t . Moreover, a relative measure of invasion risk may still be quite pertinent for a common use of pest risk maps and models (Venette et al. 2010; Yemshanov et al. 2012): to prioritize locations for surveillance or other pest management activities.

While we have proposed that network models may be especially useful for mapping pest risk, they, like other types of models, should be subject to critical scrutiny prior to their application. We see the presented approach as being primarily of interest to analysts tasked with constructing network models. The approach does not address key questions that arise in uncertainty analysis regarding how uncertainty propagates to the model outputs, or the resulting implications for decision makers who will utilize these outputs. Instead, it is merely intended to help analysts assess the fundamental soundness of their models and feel more confident about incorporating them into their analytical toolsets.

Conclusions

Because human activities contribute significantly to the proliferation of invasive species, modelling approaches that characterize important human-mediated dispersal pathways may be highly applicable for pest risk analysis. To provide a working example, we developed a geographically explicit network model that depicts the potential spread of forest pests in firewood moved by camper travel across the U.S. and Canada. We then presented an approach, based on common sensitivity analysis techniques, for assessing how this network model behaves when uncertainty is introduced into critical model aspects. In our case, the approach allowed us to determine that the model behaved consistently and predictably in the presence of uncertainty. The approach is analytically straightforward, and should be generalisable to other network models with comparable formulations.

Acknowledgements

We thank Judith Pasek (USDA APHIS, retired) and David Kowalski (USDA APHIS) for providing the NRRS data, as well as Roger Magarey (North Carolina State University) and Daniel Borchert (USDA APHIS) for their assistance with the project. The participation of Denys Yemshanov was supported by an interdepartmental NRCan - CFIA Forest Invasive Alien Species initiative.

References

- Allen A (2003) Environmental planning and management of the peri-urban interface: perspectives on an emerging field. *Environment and Urbanization* 15: 135–148. doi: 10.1177/095624780301500103
- Andow DA, Kareiva PM, Levin SA, Okubo A (1990) Spread of invading organisms. *Landscape Ecology* 4: 177–188. doi: 10.1007/BF00132860
- Carlton JT, Ruiz GM (Eds) (2003) Invasive species: vectors and management strategies. Island Press, Washington, D.C., 484 pp.
- Crosetto M, Tarantola S (2001) Uncertainty and sensitivity analysis: tools for GIS-based model implementation. *International Journal of Geographical Information Science* 15: 415–437. doi: 10.1080/13658810110053125
- Filbey M, Kennedy C, Wilkinson J, Balch J (2002) Halting the invasion: state tools for invasive species management. Environmental Law Institute, Washington, D.C., 112 pp.
- Floerl O, Inglis GJ, Dey K, Smith A (2009) The importance of transport hubs in stepping-stone invasions. *Journal of Applied Ecology* 46: 37–45. doi: 10.1111/j.1365-2664.2008.01540.x
- Getis A, Ord JK (1992) The analysis of spatial association by use of distance statistics. *Geographical Analysis* 24: 189–206. doi: 10.1111/j.1538-4632.1992.tb00261.x
- Haack RA, Petrice TR, Wiedenhoft AC (2010) Incidence of bark- and wood-boring insects in firewood: a survey at Michigan's Mackinac Bridge. *Journal of Economic Entomology* 103: 1682–1692. doi: 10.1603/EC10041
- Haack RA, Uzunovic A, Hoover K, Cook JA (2011) Seeking alternatives to probit 9 when developing treatments for wood packaging materials under ISPM No. 15. *EPPO Bulletin* 41: 39–45. doi: 10.1111/j.1365-2338.2010.02432.x
- Harwood TD, Tomlinson I, Potter CA, Knight JD (2010) Dutch elm disease revisited: past, present and future management in Great Britain. *Plant Pathology* 220: 3353–3361. doi: 10.1111/j.1365-3059.2010.02391.x
- Hastings A (1996) Models of spatial spread: a synthesis. *Biological Conservation* 78: 143–148. doi: 10.1016/0006-3207(96)00023-7
- Hastings A, Cuddington K, Davies KF, Dugaw CJ, Elmendorf S, Freestone A, Harrison S, Holland M, Lambrinos J, Malvadkar U, Melbourne BA, Moore K, Taylor C, Thomson D (2005) The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters* 8: 91–101. doi: 10.1111/j.1461-0248.2004.00687.x

- Hauser CE, McCarthy MA (2009) Streamlining ‘search and destroy’: cost-effective surveillance for invasive species management. *Ecology Letters* 12: 683–692. doi: 10.1111/j.1461-0248.2009.01323.x
- Helton JC, Davis FJ (2002) Illustration of sampling-based methods for uncertainty and sensitivity analysis. *Risk Analysis* 22: 591–622. doi: 10.1111/0272-4332.00041
- Horan RD, Perrings C, Lupi F, Bulte EH (2002) Biological pollution prevention strategies under ignorance: the case of invasive species. *American Journal of Agricultural Economics* 84: 1303–1310. doi: 10.1111/1467-8276.00394
- Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18. doi: 10.1111/j.1365-2664.2008.01600.x
- Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology* 45: 403–414. doi: 10.1111/j.1365-2664.2007.01442.x
- Jacobi WR, Goodrich BA, Cleaver CM (2011) Firewood transport by national and state park campers: a risk for native or exotic tree pest movement. *Arboriculture & Urban Forestry* 37: 126–138
- Kaluza P, Kölzsch A, Gastner MT, Blasius B (2010) The complex network of global cargo ship movements. *Journal of the Royal Society Interface* 7: 1093–1103. doi: 10.1098/rsif.2009.0495
- Karlin S, Taylor HM (1975) A first course in stochastic processes. Academic Press, New York, 557 pp.
- Keller RP, Frang K, Lodge DM (2008) Preventing the spread of invasive species: economic benefits of intervention guided by ecological predictions. *Conservation Biology* 22: 80–88. doi: 10.1111/j.1523-1739.2007.00811.x
- Koch FH, Yemshanov D, Magarey RD, Smith WD (2012) Dispersal of invasive forest insects via recreational firewood: a quantitative analysis. *Journal of Economic Entomology* 105: 438–450. doi: 10.1603/EC11270
- Koch FH, Yemshanov D, McKenney DW, Smith WD (2009) Evaluating critical uncertainty thresholds in a spatial model of forest pest invasion risk. *Risk Analysis* 29: 1227–1241. doi: 10.1111/j.1539-6924.2009.01251.x
- Lewis MA, Pacala S (2000) Modeling and analysis of stochastic invasion processes. *Journal of Mathematical Biology* 41: 387–429. doi: 10.1007/s002850000050
- Li H, Wu J (2006) Uncertainty analysis in ecological studies: an overview. In: Wu J, Jones KB, Li H, Loucks OL (Eds) *Scaling and uncertainty analysis in ecology: methods and applications*. Springer, Dordrecht, The Netherlands, 43–64.
- Moran PAP (1950) Notes on continuous stochastic phenomena. *Biometrika* 37: 17–23. doi: 10.1093/biomet/37.1-2.17
- Morgan MG, Henrion M (1990) *Uncertainty: a guide to dealing with uncertainty in quantitative risk and policy analysis*. Cambridge University Press, New York, NY, 332 pp. doi: 10.1017/CBO9780511840609

- Moslonka-Lefebvre M, Finley A, Dorigatti I, Dehnen-Schmutz K, Harwood T, Jeger MJ, Xu X, Holdenrieder O, Pautasso M (2011) Networks in plant epidemiology: from genes to landscapes, countries, and continents. *Phytopathology* 101: 392–403. doi: 10.1094/phyto-07-10-0192
- Muirhead JR, Leung B, van Overdijk C, Kelly DW, Nandakumar K, Marchant KR, MacIsaac HJ (2006) Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. *Diversity and Distributions* 12: 71–79. doi: 10.1111/j.1366-9516.2006.00218.x
- Nathan R (2006) Long-distance dispersal of plants. *Science* 313: 786–788. doi: 10.1126/science.1124975
- Nathan R, Perry G, Cronin JT, Strand AE, Cain ML (2003) Methods for estimating long-distance dispersal. *Oikos* 103: 261–273. doi: 10.1034/j.1600-0706.2003.12146.x
- Perry JN, Liebhold AM, Rosenberg MS, Dungan J, Miriti M, Jakomulska A, Citron-Pousty S (2002) Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography* 25: 578–600. doi: 10.1034/j.1600-0587.2002.250507.x
- Petrice TR, Haack RA (2006) Effects of cutting date, outdoor storage conditions, and splitting on survival of *Agrilus planipennis* (Coleoptera: Buprestidae) in firewood logs. *Journal of Economic Entomology* 99: 790–796. doi: 10.1603/0022-0493-99.3.790
- Poland TM, McCullough DG (2006) Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry* 104: 118–124
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, Widmer KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305–332. doi: 10.1146/annurev.ecolsys.32.081501.114037
- Sharov AA, Liebhold AM (1998) Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. *Ecological Applications* 8: 1170–1179. doi: 10.1890/1051-0761(1998)008[1170:MOSTSO]2.0.CO;2
- Tobin PC, Diss-Torrance A, Blackburn LM, Brown BD (2010) What does “local” firewood buy you? Managing the risk of invasive species introduction. *Journal of Economic Entomology* 103: 1569–1576. doi: 10.1603/EC10140
- USDA Animal and Plant Health Inspection Service (2011) Risk assessment of the movement of firewood within the United States. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine, Center for Plant Health Science and Technology, Plant Epidemiology and Risk Analysis Laboratory, Raleigh, NC, 122 pp.
- Venette RC, Cohen SD (2006) Potential climatic suitability for establishment of *Phytophthora ramorum* within the contiguous United States. *Forest Ecology and Management* 231: 18–26. doi: 10.1016/j.foreco.2006.04.036
- Venette RC, Kriticos DJ, Magarey RD, Koch FH, Baker RHA, Worner SP, Raboteaux NNG, McKenney DW, Dobesberger EJ, Yemshanov D, Barro PJD, Hutchison WD, Fowler G, Kalaris TM, Pedlar J (2010) Pest risk maps for invasive alien species: a roadmap for improvement. *BioScience* 60: 349–362. doi: 10.1525/bio.2010.60.5.5

- Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology & Evolution* 24: 136–144. doi: 10.1016/j.tree.2008.10.007
- Yemshanov D, Koch FH, Lyons DB, Ducey M, Koehler K (2012) A dominance-based approach to map risks of ecological invasions in the presence of severe uncertainty. *Diversity and Distributions* 18: 33–46. doi: 10.1111/j.1472-4642.2011.00848.x
- Zeckhauser RJ, Viscusi WK (1990) Risk within reason. *Science* 248: 559–564. doi: 10.1126/science.2333509

Quantifying uncertainty in pest risk maps and assessments: adopting a risk-averse decision maker's perspective

Denys Yemshanov¹, Frank H. Koch², Mark J. Ducey³,
Robert A. Haack⁴, Marty Siltanen¹, Kirsty Wilson¹

1 Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, 1219 Queen Street East, Sault Ste. Marie, ON P6A 2E5, Canada **2** USDA Forest Service, Southern Research Station, Eastern Forest Environmental Threat Assessment Center, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA

3 University of New Hampshire, Department of Natural Resources and the Environment, 114 James Hall, Durham, NH 03824, USA **4** USDA Forest Service, Northern Research Station, 1407 S. Harrison Road, East Lansing, MI 48823, USA

Corresponding author: Denys Yemshanov (dyemshan@nrcan.gc.ca)

Academic editor: S. Worner | Received 18 September 2012 | Accepted 7 March 2013 | Published 13 September 2013

Citation: Yemshanov D, Frank FH, Ducey MJ, Haack RA, Siltanen M, Wilson K (2013) Quantifying uncertainty in pest risk maps and assessments: adopting a risk-averse decision maker's perspective. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 193–218. doi: [10.3897/neobiota.18.4002](https://doi.org/10.3897/neobiota.18.4002)

Abstract

Pest risk maps are important decision support tools when devising strategies to minimize introductions of invasive organisms and mitigate their impacts. When possible management responses to an invader include costly or socially sensitive activities, decision-makers tend to follow a more certain (i.e., risk-averse) course of action. We presented a new mapping technique that assesses pest invasion risk from the perspective of a risk-averse decision maker.

We demonstrated the method by evaluating the likelihood that an invasive forest pest will be transported to one of the U.S. states or Canadian provinces in infested firewood by visitors to U.S. federal campgrounds. We tested the impact of the risk aversion assumption using distributions of plausible pest arrival scenarios generated with a geographically explicit model developed from data documenting camper travel across the study area. Next, we prioritized regions of high and low pest arrival risk via application of two stochastic ordering techniques that employed, respectively, first- and second-degree stochastic dominance rules, the latter of which incorporated the notion of risk aversion. We then identified regions in the study area where the pest risk value changed considerably after incorporating risk aversion.

While both methods identified similar areas of highest and lowest risk, they differed in how they demarcated moderate-risk areas. In general, the second-order stochastic dominance method assigned lower risk rankings to moderate-risk areas. Overall, this new method offers a better strategy to deal with the uncertainty typically associated with risk assessments and provides a tractable way to incorporate decision-making preferences into final risk estimates, and thus helps to better align these estimates with particular decision-making scenarios about a pest organism of concern. Incorporation of risk aversion also helps prioritize the set of locations to target for inspections and outreach activities, which can be costly. Our results are especially important and useful given the huge number of camping trips that occur each year in the United States and Canada.

Keywords

Risk aversion, stochastic dominance, decision-making under uncertainty, pest risk mapping, firewood movement, pathway invasion model

Introduction

Management of invasive species populations often requires making decisions about allocating scarce resources for surveillance or eradication of newly detected incursions. To aid in the decision-making process, agencies responsible for monitoring and controlling invasive species, such as the USDA Animal and Plant Health Inspection Service (APHIS) in the U.S. (APHIS 1999; Lance 2003) or the Canadian Food Inspection Agency (CFIA) in Canada (CFIA 2001), routinely assess the projected risk impacts of alien organisms on biological resources, trade and other economic activities (Simberloff 2005, Venette et al. 2010, Magarey et al. 2011). These risk assessments are usually based on the best available information about their target organisms. In general, knowledge about an organism's likely behaviour in its new environment is rarely complete, so any assessment of the potential risks and impacts includes a considerable amount of uncertainty. Consequently, a management decision based on such an assessment is dependent not only on the estimates of pest invasion risk and potential impacts but also on how the decision-makers perceive the uncertainty embedded in these estimates.

In cases where the need to manage invasive pest populations prompts calls for irreversible, costly or socially sensitive actions, decision-makers tend to follow a more certain course of action, thus exhibiting risk-averse behaviour (Gigerenzer 2002, Shefrin and Belotti 2007). Risk-averse behaviour may also be a response to a common situation when public appeals to eradicate or slow the spread of a recently detected invasive pest do not allow enough time to acquire the data necessary to adequately characterize the behaviour of the new invader. Often, the pressure to "do something" about expanding pest populations creates another incentive for decision-makers to follow a cautious, risk-averse strategy; basically, since resources for managing pest populations are limited, choices with a more certain chance of slowing the spread or eradicating new pest incursions are more likely to be adopted. Notably, government agencies tasked with monitoring and regulating the incursion and spread of unwanted

invasive organisms are fundamentally risk-averse and have resources and legal power to minimize risks, even at the cost of regulating trade or other related economic activities.

When decision-makers follow a risk-averse strategy, the presence of uncertainty in pest risk assessments inevitably changes decision outcomes about managing the pests. However, uncertainty has rarely been represented in assessments of new pest incursions in a geographical domain. At best, pest risk maps presented uncertainty as separate maps or a combination of coarse risk-uncertainty classes (Koch et al. 2009, Yemshanov et al. 2009). This kind of risk mapping implicitly places the burden of addressing uncertainty on decision-makers which, in turn, may lead to risk-averse behaviour, biased assessments and sometimes ignorance (i.e., a wait-and-see strategy if the assessment of pest impact is highly uncertain). Ideally, the uncertainty associated with the estimated impact of an invasive organism should be directly incorporated into the species' risk map by the analyst, rather than interpreted by the decision-maker (Venette et al. 2010).

In this paper, we present a new risk mapping technique that helps quantify uncertainty in pest risk assessments from the perspective of a risk-averse decision maker. We consider a particular case of risk mapping when a decision-maker faces the problem of prioritizing a set of locations in a geographical domain based on imprecise estimates of the likelihood of pest arrival in a given area. Our goal with this paper is to present the method of prioritizing uncertain outcomes of ecological invasions that would agree with a risk-averse decision-making strategy, and also to explore how the notion of risk-aversion changes the delineation of pest risk in a geographical domain.

Methods

The risk aversion concept

In general, humans tend to place relatively low weights on uncertain outcomes and relatively high weights on certain outcomes (Kahneman and Tversky 1979, Kahneman et al. 1982). Prior studies have demonstrated risk aversion in decision-making attitudes over a range of anticipated economic losses (Markowitz 1952, Levy and Levy 2001, Levy 1998). Risk-averse decision-making is not limited to cases that involve economic losses (such as allocation of investment assets), but also applies to the general case of how humans perceive valuable outcomes under uncertain conditions. The expected utility hypothesis (Arrow 1971, Schoemaker 1982) considers preferences of individuals with regard to uncertain outcomes and represents these as a function of the payouts (whether in monetary or other valuable equivalents). The expected utility theory implies that rational individuals act to maximize their expected utility (i.e., a monetary or non-monetary value that the decision-making agent attributes to a specific asset, service or action). When the expected utility value is represented as a function of the payouts in a monetary or non-monetary equivalent, this condition implies that the function is increasing (i.e., the decision-maker always prefers more to less). Adding the risk aver-

sion assumption (which implies that individuals prefer the more certain choice of two outcomes with the same expected value) adds the condition that the decision-maker's expected utility function (EUF) is concave (Fig. 1; a more detailed discussion about risk-aversion and the concavity of the EUF can be found in Arrow 1971 and Levy 1998).

The notion of risk-averse decision preferences can be embedded into the process of mapping risks of pest invasions. In our case, the concept of payoff can be thought as analogous to estimating anticipated losses from an invasive organism (or the likelihood of an organism's arrival). Conceptually, the EUF value (Fig. 1) can be interpreted as analogous to a decision-making priority that indicates the degree of importance for the decision-maker of a particular geographical site that is under risk of infestation. Clearly, any rational decision-maker would assign a higher priority to geographical locations with a higher and more certain likelihood (or anticipated impact) of invasion. By adding the notion of risk-aversion we imply that the assessment of pest invasion risk should be done from the point of view of a decision-maker whose EUF is concave. In short, the notion of risk-aversion means that pest risk assessments (which, in our case as well as in general, translate to prioritization schemes) should include some sort of penalty for uncertain choices.

The use of the EUF's concavity assumption for representing risk-averse behaviour offers a formal treatment of risk aversion without the need to explicitly define the shape of the utility function. Essentially, the concavity condition is a very basic definition of general risk-averse preferences (i.e., by eliminating the cases when the decision-maker is risk-neutral or risk-seeking) and does not define a specific range of risk-averse preferences (such as moderate to extreme risk aversion). While it is possible to impose further restrictive assumptions on the type of risk-averse behaviour – for instance, by assuming a particular functional form of the EUF or limiting the degree of risk aversion to an upper and lower bounds (Meyer 1977, Meyer et al. 2009, Hardaker et al. 2004) – estimating the shape of the EUF in the invasive species management context could be problematic given the wide variety of pest invasion problems and the diverse spectrum of decision-making skills among pest management professionals.

Prioritizing pest invasion risk under the notion of risk-aversion

We consider a pest risk map that prioritizes geographical locations across a landscape based on the likelihood that the pest will arrive at a previously non-invaded locale. Ultimately, the assignment of decision-making priorities to a particular geographical location may depend on the decision-maker's perception of uncertainty in the assessment of the impact of the pest invasion. In this paper, we explore how the incorporation of risk-averse decision preferences changes the prioritization of areas of high and low pest invasion risk in a geographical setting. We use distributions of plausible invasion scenarios generated by a stochastic model to predict the movement of an invasive organism across a heterogeneous landscape. We then delineate regions of high and low risk of pest arrival across the landscape via the application of two simple stochas-

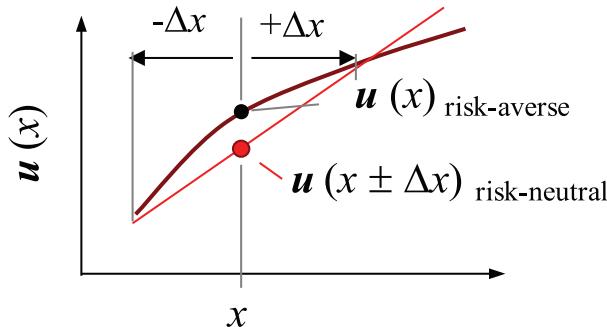


Figure 1. The expected utility function (EUF) concept. The EUF value can be interpreted as analogous to a decision-making priority that indicates the degree of importance for the decision-maker of a particular geographical site that is under risk of infestation. Bold line depicts an example of a concave EUF that denotes risk-averse decision-making preferences. The concavity condition means that a more certain amount of valuables (or degree of importance for the decision-maker) ($u(x)$) would always be preferred over a less certain choice ($u(x \pm \Delta x)$ with the same expected value, x . Dashed line shows an example EUF for a risk-neutral decision-maker (i.e., one who is indifferent between more certain and less certain choices with the same expected value).

tic ordering techniques, one of which incorporates the notion of risk aversion. For consistency, we use ordering techniques from the same family based on the stochastic dominance (SD) rule. Finally, we identify geographical regions in a landscape where adding the notion of risk aversion changes the location's pest risk value considerably.

Stochastic dominance (SD) rule

The stochastic dominance rule is a form of stochastic ordering that compares a pair of distributions. The concept was previously applied to compare distributions of investment portfolio returns in financial valuation studies (Hanoch and Levy 1969, Rothschild and Stiglitz 1970) and shares many technical aspects with the partial ordering of vectors and majorization theory in statistics (Whitemore and Findlay 1978, Levy 1992). The SD rule compares two distributions based on their cumulative distribution functions, or CDFs (Levy 1998). In our case, we compare two map locations, f and g , in a geographical setting. At each location, the multitude of plausible invasion outcomes is described by the distributions, $f(\varphi_{ij})$ or $g(\varphi_{ij})$, of the rates of invasive pest arrival, φ_{ij} , at locations f and g (Fig. 2) over an interval of possible arrival rate values, $[a; b]$, where $a = 0$ (i.e., the likelihood of pest arrival is zero) and $b = 1$ (i.e., the arrival of the pest is certain.). The SD test compares the distributions at f and g as represented by their respective cumulative distribution functions, $F(\varphi_{ij}) = \int_a^{\varphi_{ij}} f(\varphi_{ij})d\varphi$ and $G(\varphi_{ij}) = \int_a^{\varphi_{ij}} g(\varphi_{ij})d\varphi$. Location f dominates g by the first-degree stochastic dominance rule (FSD) if

$$G(\varphi_{ij}) - F(\varphi_{ij}) \geq 0 \text{ for all } \varphi_{ij}, \text{ and } G(\varphi_{ij}) - F(\varphi_{ij}) > 0 \text{ for at least one } \varphi_{ij} \quad (1)$$

The FSD rule implies that the CDFs of f and g do not cross each other (Fig. 2A). The test for FSD also supposes that a decision-maker will always prefer the “higher-value” outcome (Levy 1998) at any realization of φ_{ij} , i.e., will place a greater management priority on a location with higher likelihood of pest arrival (depicted by estimates of φ_{ij}) than a location with lower likelihood.

The FSD conditions may fail when differences between $G(\varphi_{ij})$ and $F(\varphi_{ij})$ are small. Alternatively, second-degree stochastic dominance (SSD) provides weaker but more selective discrimination by comparing the integrals of the CDFs for $F(\varphi_{ij})$ and $G(\varphi_{ij})$: $\int_a^{\varphi_{ij}} F(\varphi_{ij})d\varphi$ and $\int_a^{\varphi_{ij}} G(\varphi_{ij})d\varphi$. Location f dominates the alternative g by SSD if

$$\int_a^{\varphi_{ij}} [G(\varphi_{ij}) - F(\varphi_{ij})]d\varphi \geq 0 \text{ for all } \varphi_{ij} \text{ and}$$

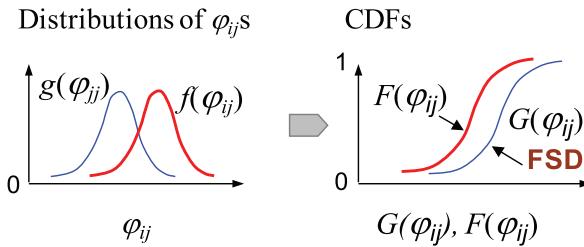
$$\int_a^{\varphi_{ij}} [G(\varphi_{ij}) - F(\varphi_{ij})]d\varphi > 0 \text{ for at least one } \varphi_{ij} \quad (2)$$

The SSD rule implies that the integrals of the CDFs for $F(\varphi_{ij})$ and $G(\varphi_{ij})$ do not cross (Fig. 2B). The SSD condition adds the assumption that the decision-maker is risk-averse, that is the dominance relationships based on the SSD rule (Eq. 2) satisfy the assumption that the decision-maker’s EUF is concave (Levy 1992, Meyer et al. 2005, Gasbarro et al. 2009, see proofs and more details in Levy 1998 and Levy and Levy 2001).

The SSD and FSD tests are pairwise comparisons. However, our study required evaluating a set of N multiple geographical locations, or map elements, that constituted a landscape. For each rule, we applied multiple pairwise stochastic dominance tests of map elements to delineate a subset of elements, \hat{A}_1 , from the total set N such that each element of \hat{A}_1 could not be dominated by any element in the rest of the set, $N - \hat{A}_1$. Formally, a non-dominant subset \hat{A}_1 is equivalent to an “efficient set” in financial investment valuation literature (Fishburn and Vickson 1978, Porter et al. 1973, Porter 1978, Post and Versijp 2007). While financial investment analyses often focus on evaluating a single non-dominant set and narrowing down the multitude of possible investment scenarios to the fewest possible choices, our study required evaluating each element (map location) in a set. Hence, we evaluated all nested non-dominated subsets (based on the FSD or SSD rules) in the total set N using the following algorithm (Goldberg 1989): After the first non-dominant subset \hat{A}_1 was found, it was assigned the highest invasion risk rank of 1 and removed from set N temporarily. Then, the next non-dominant subset was found from the rest of the set, $N - \hat{A}_1$, assigned a risk rank of 2, temporarily removed from set $N - \hat{A}_1$ and so on. The delineation of nested non-dominant sets continued until all elements in the set N were evaluated and assigned a corresponding decision-making priority rank. The final rank values based on the FSD and SSD rules were then plotted back to their geographical locations, resulting in a map for each SD rule.

The stochastic dominance rule assumes a very broad range of decision-making behaviours and has relatively low ability to discriminate small non-dominant sets. To improve the discriminative capacity, some alternative metrics have been proposed.

A. First-degree stochastic dominance (FSD):



B. Second-degree stochastic dominance (SSD):

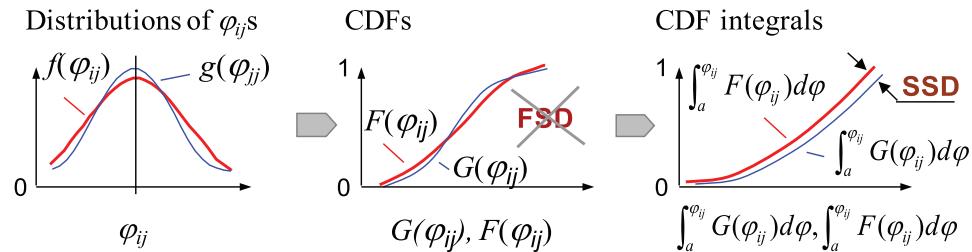


Figure 2. First-degree and second-degree stochastic dominance rules: **A** distributions, $f(\varphi_{ij})$ and $g(\varphi_{ij})$, of camper travel probabilities (φ_{ij}) at two corresponding map locations, f and g **B** the cumulative distribution functions (CDFs), $F(\varphi_{ij})$ and $G(\varphi_{ij})$, of $f(\varphi_{ij})$ and $g(\varphi_{ij})$ in Fig. 1(a). “FSD” indicates the first-degree stochastic dominance conditions are satisfied (i.e., $G(\varphi_{ij})$ and $F(\varphi_{ij})$ do not cross each other) **C** two additional example distributions of pest arrival rates at f and g **D** in this case, CDFs of $f(\varphi_{ij})$ and $g(\varphi_{ij})$ cross each other so that the first-degree stochastic dominance conditions fail **E** the integrals, $\int_a^{\varphi_{ij}} G(\varphi_i) d\varphi$, $\int_a^{\varphi_{ij}} F(\varphi_i) d\varphi$, of the CDFs. “SSD” indicates the second-degree stochastic dominance conditions are met (i.e., $\int_a^{\varphi_{ij}} F(\varphi_i) d\varphi$ and $\int_a^{\varphi_{ij}} G(\varphi_i) d\varphi$ do not cross each other).

The stochastic dominance with respect to a function, or SDRF (Meyer 1977), assumes that the absolute risk aversion measures of the decision-maker lie between arbitrarily defined lower and upper bounds. Another measure, the stochastic efficiency with respect to a function, or SERF (Hardaker et al. 2004; Hardaker and Lien 2010), ranks risky alternatives in terms of certainty equivalents (CE) while assuming that the degree of risk aversion varies within a defined range. The SERF method requires making additional assumptions about the functional form of a decision-maker’s expected utility function and assumes that the decision-maker’s risk aversion metric is of the same functional form as those lower and upper risk aversion bounds. Imposing these additional restrictions on risk-averse preferences enables the SERF metric to discriminate even smaller non-dominant sets than the stochastic dominance rule but requires eliciting the risk aversion bounds from decision-makers and identifying the functional form of the EUF. In our risk mapping case, these details about risk-averse preferences were unavailable, so we opted to use the more generalized but less discriminating SSD rule.

Case study

We explored the impact of decision-maker risk-aversion with a North American case study that estimates the likelihood of wood-boring forest pests arriving in firewood at campgrounds on U.S. federal lands in the 49 U.S. states by travellers from the continental U.S. and Canada. The potential for accidental, long-distance transport of alien species with recreational travel has become a topic of considerable concern in North America (Haack et al. 2010, Tobin et al. 2010, Jacobi et al. 2011, Koch et al. 2012). Visitors often bring untreated firewood to parks and campgrounds in the U.S. and Canada, and this material has been recognized as a significant vector of wood-boring forest pests (CFIA 2011, APHIS 2010, The Nature Conservancy 2011, Jacobi et al. 2011). For example, movement of firewood by campers has been deemed one of the major causes of the rapid expansion of populations of the emerald ash borer, an invasive pest of ash trees (*Fraxinus spp.*), throughout eastern Canada and the U.S. Midwest (Haack et al. 2002, 2010, Kovacs et al. 2010). Overall, recreational travel is considered a significant vector of firewood movement: campground surveys in various parts of the U.S. indicate that 8–57% of campers bring their own firewood from home, frequently travelling distances exceeding 160–320 km and crossing state and U.S.-Canada border lines (APHIS 2011). Moreover, staff at national, state and provincial campgrounds typically have scarce resources to check campers for firewood usage and lack the legal mandate to undertake random checks of firewood in visitors' vehicles. This makes it difficult to enforce preventive measures such as bans on the importation and use of outside firewood.

While the problem of moving forest pests with firewood is well recognized (APHIS 2010, The Nature Conservancy 2011), data on the movement of firewood across North America are generally lacking. Therefore, we undertake an alternative approach by exploring more general travel patterns of campers rather than their actual movement of firewood. For this study, we analyzed a 5-year (2004–2009) geographically referenced database of campground visits in the United States (including visits from Canada). Our primary data source for this study was the National Recreation Reservation Service (NRRS), which manages reservations for campgrounds at over 1700 locations that are operated by the U.S. Army Corps of Engineers, the USDA Forest Service, the National Park Service, and other federal agencies (see full description of the NRRS database in Koch et al. 2012). Each reservation record provided information including the name and state of the destination campground, reservation date, and the visitor's origin ZIP code (or postal code for Canadian visitors). The NRRS data set provided geographic coordinates for the campgrounds, and we assigned geographic coordinates for each visitor's home ZIP code (or postal code) in the data set (ESRI 2009, NRCan 2010). These records were then used to build a network of pathways that connected sets of origin and destination locations across North America (see further details in Koch et al. 2012).

Pathway model

We used the NRSS data set to undertake spatial stochastic pathway simulations of potential movements of invasive pests with firewood carried by campers. Spatial stochastic models have been increasingly used for assessing risks of ecological invasions (Rafoss 2003, Cook et al. 2007, Pitt et al. 2009, Muirhead et al. 2006, Yemshanov et al. 2009, 2010). We applied a pathway model that used vector-based information stored in the NRSS database to predict movements of recreational travellers to federal campgrounds in the U.S., including cross-border visits from Canada. Here, we assumed that there is a predictable relationship between camper travel and firewood usage (Jacobi et al. 2011), so the camper travel pattern is a proxy for the firewood transport pattern.

Our choice of a network-based model was aimed at emphasizing the importance of human-assisted movement of invasive organisms over long distances, a phenomenon that many classical dispersal models cannot predict well (see Andow et al. 1990, Buchan and Padilla 1999, Melbourne and Hastings 2009). The model is conceptually similar to that presented in Yemshanov et al. (2012a, b); here, we describe only the model updates required for this study.

We used the NRSS dataset to build a matrix of $n \times n$ origin–destination locations, where each matrix element defined the number of visits for a particular pair of origin–destination locations (i.e., the total number of reservations between a particular origin ZIP code and destination campground). Because the original NRSS records encompassed more than 500 000 unique spatial locations, we aggregated the data to a grid of 15 × 15 km cells. This aggregation decreased the size of the matrix and reduced the computational burden. The NRSS data were then parsed into a set of unique pathway segments, each connecting an origin map cell, i , and a destination map cell, j , in the network. Subsequently, the cumulative number of visits (based on the NRSS reservations) for each pathway segment ij were used to build an $n \times n$ pathway matrix where each element defined the rate, p_{ij} , of camper movement (and by extension, firewood-facilitated pest transport) from cell i to cell j . The pathway matrix stored the p_{ij} values for all possible pairs of (i, j) cells in the transportation network:

$$\mathbf{P}_t = \begin{bmatrix} 0 & p_{12} & \cdots & p_{1n} & 1 - \sum_{j=1}^n p_{1j} \\ p_{21} & 0 & \cdots & p_{2n} & 1 - \sum_{j=1}^n p_{2j} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ p_{n1} & p_{n2} & \cdots & 0 & 1 - \sum_{j=1}^n p_{nj} \end{bmatrix} \quad (3)$$

where the elements $1 - \sum_{j=1}^n p_{ij}$ describe the probability that camper travel between i and j did not occur and

$$p_{ij} = m_{ij}\lambda \quad (4)$$

where m_{ij} is the total number of reservations for the origin-destination vector ij and λ is a scaling parameter.

Ideally, the scaling parameter λ would define the likelihood that a pest is moved with firewood from any location i to j . In fact, knowing the precise value of λ would be critical in order to estimate p_{ij} exactly. However, our study did not require precise estimates of λ because we had the more basic aim of prioritizing the geographical locations (i.e., map cells) according to their level of risk. In short, our goal was to order the full set of map cells in the dimension of high-low relative infestation risk via multiple pairwise tests for first- and second-degree stochastic dominance (as described in Eqs. 1 and 2). In this case, the value of λ needed only to be sufficiently small to ensure that the sum of transmission rate values in the \mathbf{P}_t matrix rows was below 1:

$$\sum_{j=1}^n p_{ij} \leq 1 \quad (5).$$

We then used the \mathbf{P}_t matrix to generate stochastic realizations of potential movements of campers (and by extension, pest-infested firewood) from a given cell i to other cells with recreational travel. With i set as the point of “origin”, the model simulated subsequent camper movements from i to other destination cells j by extracting the transmission probabilities from \mathbf{P}_t associated with i (Fig. 3). The process continued until a selected destination node had no outgoing paths or a terminal state was chosen based on the elements $1 - \sum_{j=1}^n p_{ij}$ in \mathbf{P}_t . Finally, for each pair of origin–destination locations (i, j), a transmission probability, φ_{ij} , was estimated from the number of times the camper arrived at j from i over K multiple stochastic model realizations

$$\varphi_{ij} = J_{ij}/K \quad (6)$$

where J_{ij} is the number of individual pathway simulations where a camper originated at i and ultimately arrived at j , and K is the total number of individual simulations of pathway spread from i (for this study, $K = 2 \times 10^6$ for each i). The values of φ_{ij} were estimated for each (i, j) pair of origin–destination cells, requiring a total of $K \times [n(n-1)]$ pathway simulations.

Prioritizing the geographical locations in the dimension of transmission risk

We used the transmission probabilities φ_{ij} (which, in relative terms, depict the potential of invasive pests to be moved by recreational travellers) to order the map cells across Canada and the U.S. in dimensions of high-low risk. We built separate maps for each of the continental 49 U.S. states and nine Canadian provinces (including the Yukon Territory). For each potential origin map cell, the model generated a list of other cells (with corresponding transmission probabilities φ_{ij}) to which the movement of campers (and, in turn, forest pests carried by firewood) was most likely. Since our primary

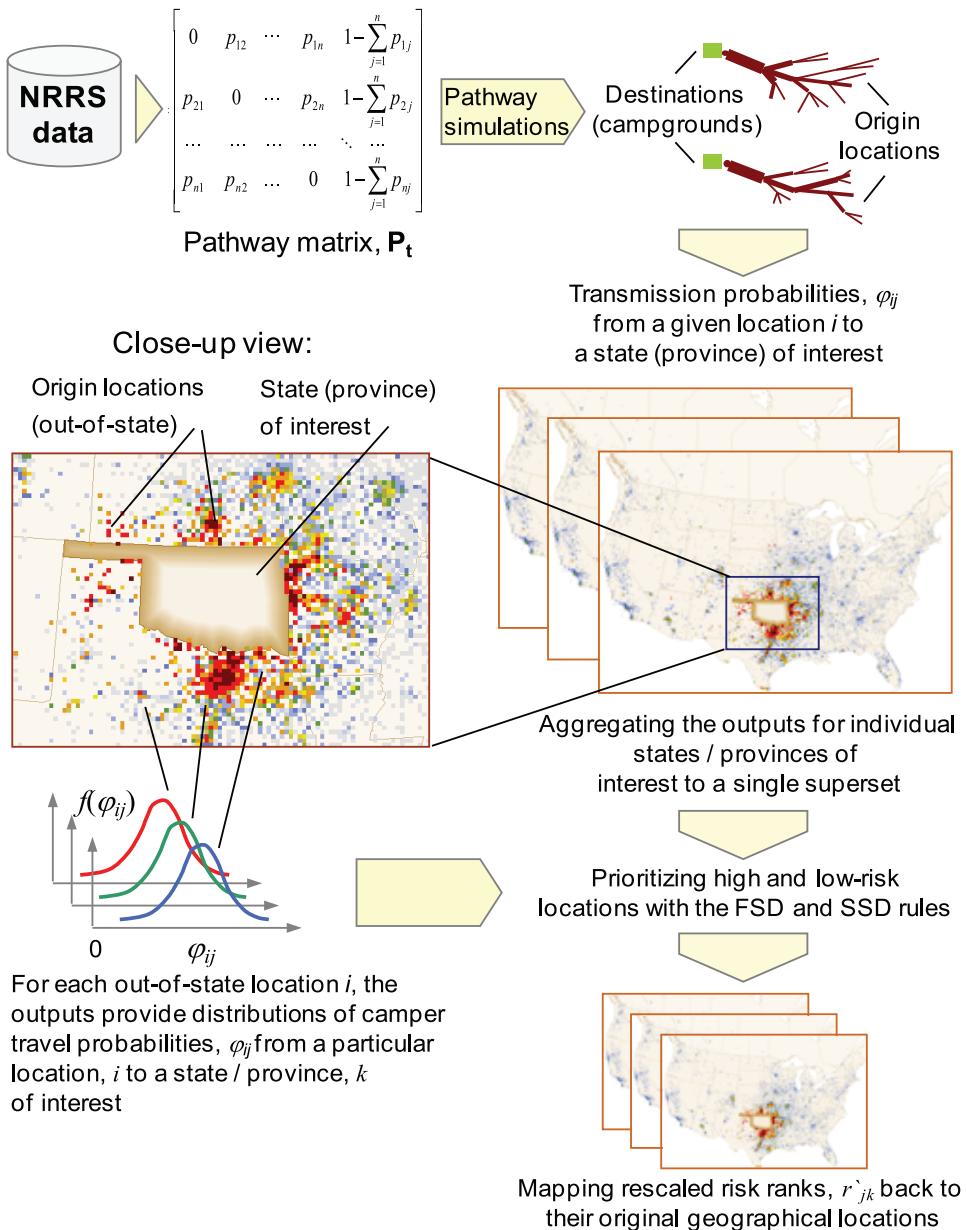


Figure 3. Mapping risks that invasive pests may be carried with infested firewood by campers (the analysis summary).

focus was to estimate the risk of pest movement to a particular state or province, we rearranged the results so each cell i outside of a state (province) of interest, k , had an associated distribution of the transmission probabilities φ_{ij} ($j \in k$), from that location to the state of interest (Fig. 3). In short, this distribution described the degree of the location's invasiveness in relation to the state (province) of interest.

Assuming that the map for each state (province) of interest k had n_k external locations that could potentially serve as sources of future pest arrivals with camper travel, the analysis produced a total (i.e., across all k) of $N = \sum_{k=1}^K n_k$ distributions of the j_{ij} transmission probability values. We then applied the FSD and SSD rules to this superset of distributions so that we could order them in the dimension of highest-to-lowest risk of transmission from i to k . Thus, each cell i was given two partial risk ranks, r_{ik}^{SSD} and r_{ik}^{FSD} , of pest movement from i to k by campers. Importantly, since partial ordering of the distributions of transmission probabilities was done in a single superset (that included all sets of outputs representing risks of movement to all k states / provinces of interest), the final risk ranks for different states and provinces can be compared one with another.

Our next goal was to compare the ranks generated with the FSD and SSD techniques and to explore how much the risk aversion assumption in the delineations based on the SSD rule changed the geographical patterns of risk across the study area. Because the SSD rule is weaker than FSD and usually produces smaller-size non-dominant sets (Porter 1978, Post 2003), the total number of nested non-dominant sets (and subsequently the number of risk ranks) in the two classifications will be different. Therefore, we inverted and rescaled the risk ranks r_{ik} generated by the FSD and SSD techniques to a 0-1 range so the rescaled ranks, r'_{ik}^{FSD} and r'_{ik}^{SSD} denoting the highest risks were close to 1 and the lowest risks were close to 0. We then explored differences between the rescaled risk ranks generated with the FSD and SSD classifications and their variation across the study area. We also plotted the rescaled risk ranks r'_{ik}^{FSD} and r'_{ik}^{SSD} as maps, each depicting the risk of pest transport to a particular state (province) with recreational travel from elsewhere.

Results

Exploratory geospatial data analysis

Figure 4 depicts example maps of the rescaled risk ranks for Texas and California generated, using the second-degree stochastic dominance rule. (The maps of risk rankings based respectively, on the first- and second-degree stochastic dominance rules for the other U.S. states and the Canadian provinces are shown in online Appendices 1 and 2). The maps suggest some basic geographic trends in campers' travel behaviour. First, the highest-risk out-of-state locations (i.e., from where the movement of infested firewood is the most likely) are usually in close proximity to the state (provincial) border or, at longer travel distances, are associated with major urban centres. In addition, prominent recreational destinations such as Grand Canyon National Park (AZ) or Zion National Park (UT) are also high-risk locations. Notably, there are distinctive regional trends in camper behaviour. For instance, interior states in the mid-western and southeastern U.S. are characterized by predominantly local and medium-range travel from surrounding areas. While states in these regions have few high-profile recreational

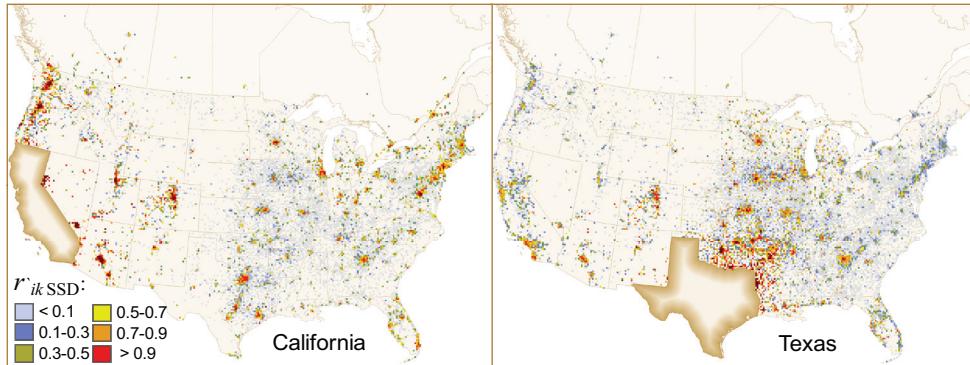


Figure 4. Examples of risk maps depicting the potential of invasive forest pests to be moved by recreational travelers to the states of Texas and California. The risk rank values are based on the second-degree stochastic dominance rule (SSD), which incorporates risk-averse decision preferences. The maps for the other U.S. states, Canadian provinces and the Yukon Territory can be found in online Appendix 2.

destinations such as national parks, they have a dense and fairly uniform network of campgrounds, situated near major water bodies or public forest lands, which are used more often by casual or short-term campers.

The western U.S. has vast areas of sparsely populated land, and so has a higher relative proportion of long-distance sources of campers (and thus potential firewood-associated pests) than the eastern U.S. The risk of pests being moved by campers returning to Canada is relatively low. However, the largest Canadian cities, such as Toronto (ON), Montreal (QC) and Vancouver (BC), have relatively high risks of being potential sources of infestations in neighbouring U.S. states.

Differences between risk ranks based on the FSD and SSD rules

We investigated the geographic differences between the risk rank maps based on the FSD and SSD criteria. Figure 5 and online Appendix 3 present maps of differences in rank values, $\Delta r'_{ik} = r'_{ik}^{\text{FSD}} - r'_{ik}^{\text{SSD}}$, composed for individual states and provinces. Overall, the FSD and SSD approaches provided similar delineations of the locations ranked with the most extreme risks, i.e., above 0.95 or below 0.05 (Table 1). The greatest differences between the ranks based on the FSD and SSD criteria were found in the areas in the peri-urban and rural zones (since information about camper travel to these locations is expected to be less certain because of a lack of well-documented links from the NRRS data).

For moderate risk ranks between 0.05 and 0.95, the methods appeared to place differing levels of emphasis on certainty in the φ_{ij} transmission probabilities. The SSD approach seemed to decrease the risk rank's value when the variation of the probability (i.e. uncertainty) was high and generally assigned lower rank values than the approach based on the FSD rule. This tendency is particularly evident in the range of moderate

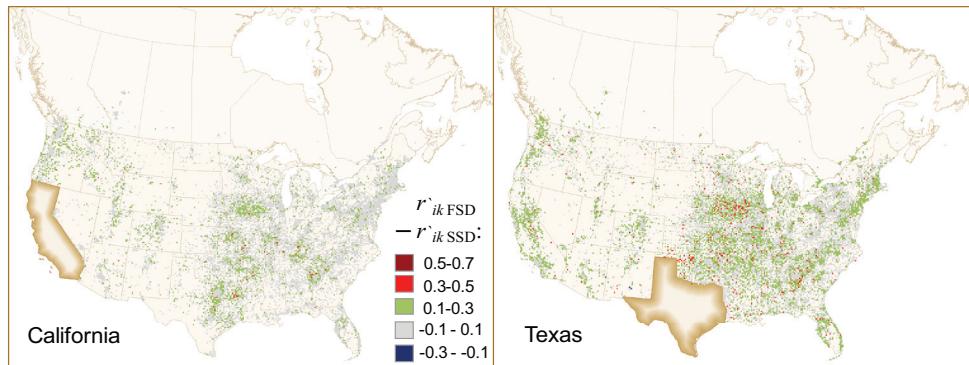


Figure 5. Maps of rank differences, $\Delta r'_{ik} = r'_{ik} \text{FSD} - r'_{ik} \text{SSD}$, between the delineations based on first- and second-degree stochastic dominance for Texas and California. Positive values indicate that the SSD-based risk rank is lower than the FSD-based rank (so adding the notion of risk aversion decreases the risk rank). The maps for the other U.S. states, Canadian provinces and the Yukon Territory can be found in online Appendix 3.

Table 1. Correspondence between the FSD and SSD rank classes as a percent of the map area. The numbers in the diagonal show the percentages of the map area where the rank class was the same in both FSD and SSD rankings. The largest percentage values in each row are marked on bold.

Risk rank based on the FSD rule	Risk rank based on the SSD rule					
	0–0.05 (lowest)	0.05–0.25	0.25–0.5	0.5–0.75	0.75–0.95	0.95–1 (highest)
0–0.05 (lowest)	100					
0.05–0.25	72.2	27.7	0.1			
0.25–0.5	0.7	89.8	7.7	1.8		
0.5–0.75		30.5	52.8	15.0	1.7	
0.75–0.95		<0.01	3.5	24.6	71.0	0.9
0.95–1 (highest)					2.6	97.4

ranks 0.05–0.5 (Table 1). For example, almost 90% of ranks assigned to a 0.25–0.5 range in the FSD classification were classified into the 0.05–0.25 range in the SSD classification. Similarly, 72% of low-risk ranks classified within the range of 0.05–0.25 in the FSD classification had an SSD rank below 0.05, and roughly 83% of locations with FSD ranks in the 0.5–0.75 range were assigned lower risk ranking in the SSD delineations (Table 1).

Online Appendix 4 presents summaries of the differences, for individual states and provinces, between the FSD and SSD ranks allocated to broad rank classes: 0–0.05, 0.05–0.25, 0.5–0.75, 0.75–0.95 and 0.95–1. Most of the changes in rank values occurred in low–medium rank classes between 0.05 and 0.5, which is consistent with Table 1. For many states and provinces, the difference between the FSD and SSD-based ranks was at least one rank class (e.g., ranks in a 0.25–0.5 range under the FSD rule were assigned to a 0.05–0.25 range under the SSD rule).

Discussion

The maps in online Appendix 3 suggest that geographical patterns of changes between the FSD and SSD rank values, $\Delta r'_{ik}$, can be grouped into three general types. The first type represents states with very high volumes of out-of-state recreational visits (and thus higher risks of pest arrival with infested firewood from elsewhere), such as California and Texas (Table 2, Appendix 3). For these states, the high $\Delta r'_{ik}$ values are uniformly distributed in rural and suburban regions across much of the entire central and western U.S. However, the difference between the FSD and SSD ranks in large urban areas appeared to be small (Fig. 5).

The second type is represented by the mountain and desert states in the western U.S. (such as Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington and Wyoming), which show a less uniform pattern of $\Delta r'_{ik}$ values. Most of the highest changes in ranks were either associated with large urban areas in the central and eastern U.S. or were dispersed across rural and suburban areas in neighbouring states in the western U.S. (Appendix 3). This bifurcated distribution of changes in rank is likely caused by some campers travelling long distances from the central and eastern U.S. and Canada (i.e., for predominantly urban areas), as opposed to shorter-distance travels for campers from neighbouring states in the western U.S.

The third group is represented by states in the northeastern U.S. (Connecticut, Delaware, Maine, Massachusetts, New Hampshire, New Jersey, New York, Rhode Island, Vermont), more sparsely populated states in the north-central U.S. (North and South Dakota), and the most populous Canadian provinces (Alberta, British Columbia, Ontario and Quebec, Appendix 3). For this group, the highest changes in risk ranks were detected only in locations close to the state or provincial border, or in major urban areas in the western U.S., such as Denver (CO), Los Angeles (CA), Phoenix (AZ) and San Francisco (CA).

The rest of the Canadian provinces, the District of Columbia and Alaska showed extremely small changes in the rank values. Note that the risk rank values for these states and provinces were very low for both the FSD- and SSD-based delineations. The rest of the U.S. states can be characterized by a combination of the geographical patterns of high $\Delta r'_{ik}$ values noted above: relatively uniform allocations across rural and peri-urban areas in a sort of “fringe zone” adjacent to the state borders, as well as long-distance travel hotspots associated with densely populated urban areas or prominent recreational destinations (e.g., national parks) in the western U.S. (Appendix 3).

Impact of adding the notion of risk aversion

The general impact of adding risk-averse decision preferences can be illustrated (Fig. 6) using a simplified delineation of risk ranks in the dimensions of mean transmission probability, $\bar{\varphi}_j$, and its degree of variation, represented by the standard deviation, $\sigma(\varphi_j)$. When uncertainty is ignored and the assignment of risk classes is based solely on

Table 2. State and provincial summaries based on the mean rank values, $r'_{ik\text{FSD}}$ and $r'_{ik\text{SSD}}$.

Country	State / Province	FSD-based risk rank		SSD-based risk rank	
		Mean $r'_{ik\text{FSD}}$	Relative rank	Mean $r'_{ik\text{SSD}}$	Relative rank
US	Texas	0.283	1	0.202	1
US	Arkansas	0.251	2	0.184	3
US	California	0.246	4	0.202	2
US	Missouri	0.246	3	0.167	4
US	Tennessee	0.226	5	0.157	5
US	Colorado	0.215	6	0.140	7
US	Georgia	0.201	8	0.143	6
US	Florida	0.205	7	0.128	8
US	Illinois	0.197	9	0.121	10
US	Iowa	0.185	10	0.123	9
US	Oklahoma	0.179	11	0.117	11
US	Washington	0.169	12	0.109	15
US	Oregon	0.168	13	0.110	14
US	Arizona	0.161	15	0.115	13
US	Utah	0.151	17	0.116	12
US	Kansas	0.166	14	0.100	17
US	North Carolina	0.150	18	0.101	16
US	Nevada	0.156	16	0.088	20
US	Kentucky	0.142	19	0.095	18
US	Alabama	0.137	21	0.093	19
US	Virginia	0.139	20	0.086	21
US	Pennsylvania	0.132	22	0.085	23
US	South Carolina	0.121	25	0.085	22
US	Idaho	0.127	23	0.081	24
US	Ohio	0.121	24	0.062	27
US	Mississippi	0.119	26	0.072	25
US	New York	0.116	27	0.063	26
US	Louisiana	0.113	29	0.062	28
US	Maryland	0.114	28	0.057	31
US	Indiana	0.111	30	0.058	30
US	West Virginia	0.092	32	0.059	29
US	Minnesota	0.106	31	0.053	33
US	Wisconsin	0.088	33	0.046	34
US	Montana	0.073	38	0.054	32
US	New Mexico	0.082	34	0.039	36
US	Michigan	0.080	35	0.037	38
US	Massachusetts	0.078	36	0.033	39
US	Nebraska	0.073	39	0.039	37
US	New Hampshire	0.067	41	0.044	35
US	New Jersey	0.075	37	0.028	41
Canada	British Columbia	0.068	40	0.024	43
US	Wyoming	0.053	44	0.031	40
Canada	Quebec	0.062	42	0.020	44
US	South Dakota	0.040	45	0.027	42

Country	State / Province	FSD-based risk rank		SSD-based risk rank	
		Mean $r'_{ik,FSD}$	Relative rank	Mean $r'_{ik,SSD}$	Relative rank
US	Connecticut	0.054	43	0.020	45
Canada	Alberta	0.028	47	0.012	46
US	Maine	0.027	48	0.012	47
Canada	Ontario	0.030	46	0.010	50
US	Vermont	0.024	49	0.010	49
US	North Dakota	0.017	51	0.010	48
US	Delaware	0.023	50	0.008	51
US	Rhode Island	0.016	52	0.006	52
US	Alaska	0.004	53	0.002	53
Canada	New Brunswick	0.001	54	0.002	54
Canada	Saskatchewan	0.001	55	0.001	55
Canada	Manitoba	0.001	56	0.001	56
Canada	Nova Scotia	<0.001	57	0.001	57
US	District of Columbia	<0.001	58	<0.001	58
Canada	Yukon Territory	<0.001	59	<0.001	59

the mean probability $\bar{\varphi}_j$, broad risk ranks can be defined by parallel lines at certain constant probability thresholds (i.e., parallel dashed lines in Fig. 6). Adding the notion of risk aversion generally implies that between two geographic locations (represented by points in Fig. 6) with the same expected mean probability of the pest's arrival, the more certain choice (i.e., the location exhibiting lower variation) will be assigned a higher decision-making priority. In turn, the boundaries between risk classes under the risk-averse SSD rule (i.e., solid lines in Fig. 6) will always be tilted at an angle, b , below 90 degrees relative to their corresponding risk-neutral boundaries, since a location with the same mean transmission probability $\bar{\varphi}_j$ as another location, but lower variability will receive a higher risk rank under SSD.

Notably, the SSD rule does not restrict the potential range of risk-averse preferences, i.e., it does not limit the degree of decision-makers' absolute risk-aversion. This suggests that the SSD rule allows for the possibility that the risk aversion of some decision-makers may be very large, such that small differences in the uncertainty of the risk estimates could receive unrealistically high importance. To address instances of extreme risk aversion, several alternative approaches that limit the potential range of risk aversion have been proposed. For example, stochastic dominance with respect to a function (SDRF) limits the range of the absolute risk aversion measure to arbitrary chosen limits (Meyer 1977; Meyer et al. 2009). Alternatively, stochastic efficiency with respect to a function (SERF) restricts the variation of the degree of risk aversion to an arbitrarily defined range but ranks risky alternatives in terms of their certainty equivalents (CE) (Hardaker et al. 2004; Hardaker and Lien 2010). The SERF method requires making additional inferences about the functional form of the expected utility function and adds the restrictive assumption that the measure of risk aversion used is held constant as the level of outcomes changes (Hardaker and Lien 2010). Overall, the SERF metric is capable of discriminat-

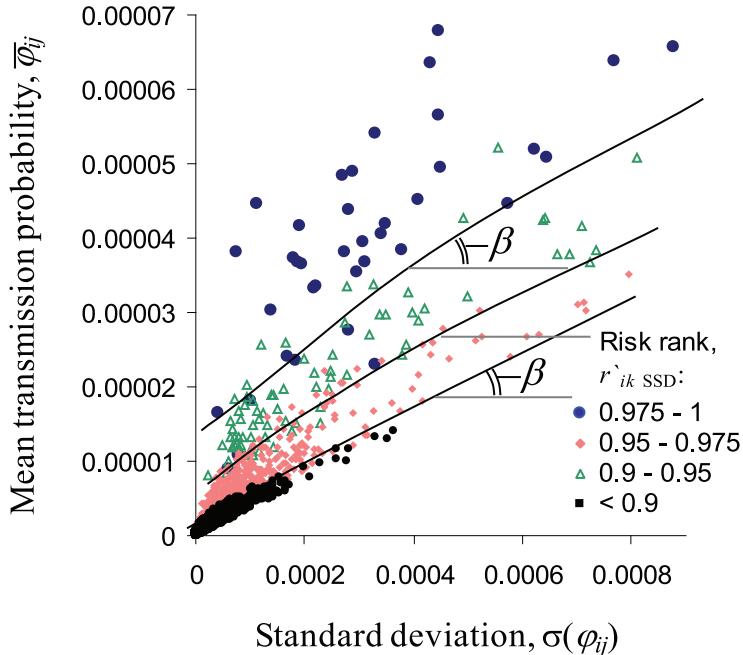


Figure 6. Schematic representation of broad risk classes delineated with the SSD rule, r'_{ik} , in dimensions of the mean camper travel probability, $\bar{\varphi}_{ij}$, and its standard deviation, $\sigma(\varphi_{ij})$. b denotes the tilt angle between the generalized boundaries of broad risk classes in the point cloud $\bar{\varphi}_{ij}$ - $\sigma(\varphi_{ij})$ and the horizontal line indicates a constant mean transmission rate ($\varphi_{ij} = \text{const}$). Dashed lines denote the boundaries between hypothetical risk classes in a risk-neutral classification (i.e., $b = 0$, when risk delineation is independent of the amount of uncertainty in the estimates). Points represent individual locations (15×15 km map cells, a 10% random subset of all locations).

ing smaller non-dominant sets than SSD (or SDRF), but this is achieved at the expense of imposing strong restrictive assumptions on decision-maker's risk-averse preferences.

In economic studies, the SSD rule has commonly been considered too coarse to be used effectively for practical purposes (Hardaker et al. 2004, Hardaker and Lien 2010). However, we found the discriminatory power of the SSD rule to be adequate for our geographical risk mapping case. Since our study required ranking of all spatial elements in the map (and the total number of map elements was very large), the performance of the SSD rule was sufficient to discriminate a large number of nested non-dominant sets and identify areas of high and low pest arrival risk with good spatial precision. Because the analysis delineated nested non-dominant sets (instead of finding a single non-dominant set of the smallest possible size), the impact of lower discriminatory capacity was less noticeable. Also, the magnitude of the variation in pest arrival rates in our study was considerably larger than the typical variability of net returns (or CE values) in economic efficiency studies, hence the differences between the CDFs were more discernible. Note that the discriminatory power of the SSD-based approach could be further improved by increasing the number of discrete percentile points in the

calculations of the CDF integrals or by re-sampling the underlying geographical data to a higher spatial resolution and thereby increasing the total number of map elements in the study area (which would lead to a larger number of nested non-dominant sets).

Technical aspects of an application of the stochastic ordering techniques

In our study, we used the stochastic dominance concept to delineate nested non-dominant sets of map elements, based on a partial order of these elements, in a space defined by the distributions of pest transmission rates φ_{ij} to a state (province) of interest. The reliance on a partial order of elements makes this approach relatively stable to errors in data and underlying assumptions about the behaviour of the invader. Basically, it takes a higher degree of error to alter the partial ordering of elements in the set and change the dominance relations between the map elements.

The stochastic dominance concept (SD) provides an attractive framework for assessing risks of pest invasions under uncertainty. In our study, the theoretical attractiveness of the second-degree stochastic dominance (SSD) lies in its non-parametric nature (Fishburn and Vickson 1978). While the SSD rule operates from the general perspective of a risk-averse decision-maker (Porter et al. 1973, Meyer et al. 2005), it does not require an explicit specification of a decision-maker's expected utility function (i.e., defining a numerical "utility" value for every possible invasion outcome that a decision-maker may encounter). In fact, the precise determination of the degree of risk aversion (as well as the other behavioural aspects of managing invasive pests) is problematic as it would require tracking the history of decision-making actions within agencies responsible for managing pest incursions, as well as quantifying the associated risk preferences. Note that practical applications of the SSD rule still require careful consideration of the decision-making problem of interest.

The stochastic ordering techniques used in this study help resolve some troublesome issues in assessing invasion risks when knowledge about an invasive organism is insufficient for deriving precise estimates of risk. A lack of knowledge about the organism's behaviour in a new environment often causes experts to generate fairly coarse assessments (e.g., by assessing risk in vague "high-low" terms or deriving a broad distribution of plausible invasion outcomes instead of a single impact value). Although experts can discern the meaningful tendencies in the predicted outcome of an invasion (such as relatively high or low likelihood of invasion), they are rarely able to assign precise likelihood values. In techniques based on nested non-dominant sets like the FSD and SSD rules, every geographic location of interest is ordered along a risk gradient, which makes the issue of assigning precise pest arrival rate values less critical.

The estimation of non-dominant sets with the FSD or SSD rule requires undertaking multiple pairwise tests for stochastic dominance and has a computational complexity on the order of $N(N - 1)/2$. While calculation of non-dominant sets for large N can be computationally demanding, the basic algorithm that checks for non-dominance is relatively simple, and can be easily parallelized.

We must note that the use of nested non-dominant sets for ordering geographic locations provides only a partial ranking (so that ranks reflect relative “high-low” positions only within a given dataset). Since our intention was to develop comparable risk rankings derived for the U.S. states, eight Canadian provinces and the Yukon Territory, we undertook the extra step of aggregating all datasets into a single superset and ranking it with the FSD and SSD rules. Thus, the final ranks were mapped within a single frame of reference and the ranks for individual states and provinces were comparable one with another. While computationally demanding, we believe this method addresses a major criticism of risk mapping methods based on a partial ordering: an inability to generate a common ranking space. Table 2 shows a comparative level of risk that each state (or province) will receive infested firewood with recreational travelers as an average rank values, r_{ik} of firewood moved to a state (or province) of interest from all out-of-state locations as a risk metric. As Table 2 suggests, Texas, Arkansas, and California show the highest potential to receive forest pests in camper-transported firewood from elsewhere, whereas the District of Columbia, Yukon Territory, Nova Scotia, Manitoba and Saskatchewan have the lowest potential. These rankings assume a generalized risk of infestation. Knowledge of a specific potential source location for an infestation could, of course, change these rankings, but the approach used here to incorporate risk aversion in the mapping process would remain applicable.

Incorporation of risk-averse preferences into a delineation of high-risk locations has some important implications for the development of broad-scale pest surveys and public outreach campaigns. In regions where the areas with high-risk estimates based on the SSD rule are uniformly dispersed in relatively close proximity to a state or provincial border (such as for Alabama or Pennsylvania, Appendix 2), the development of large-scale public outreach programs could target nearby states because camper travel is mostly local and risk is distributed uniformly in close proximity to the state (or province) of interest. Alternatively, if the majority of high-ranked source locations indicate long-distance travel destinations (such as for the prominent national parks in Utah or Arizona), a statewide surveillance program may be inefficient and an alternative effort that targets specific high-risk recreation destinations would represent a more effective strategy.

Conclusions

This study demonstrated how the notion of a decision-maker’s risk aversion can be incorporated into the process of mapping risks of ecological pest invasions. We believe that the approach based on the stochastic dominance rules represents a major step forward in model-based assessments of ecological risks because it provides a tractable way to incorporate decision-making preferences into the estimates of pest invasion risk and consecutively offers the appropriate treatment of uncertainty according to the anticipated preferences of decision-makers (the end users of risk assessments and maps). Overall, incorporation of risk-aversion adds credibility to the pest risk mapping

process, helps narrow the set of geographical locations that would need to be targeted for costly inspection and public outreach activities, and could be easily applied to the threat of recreational firewood movement in North America.

Acknowledgements

We thank the Organisation for Economic Co-operation and Development (OECD) Co-operative Research Programme (CRP) on Biological Resource Management for Sustainable Agricultural Systems for sponsoring travel to present this research at the 6th International Pest Risk Mapping Workshop in Tromsø, Norway. We also thank Judith Pasek (USDA APHIS, retired) and David Kowalski (USDA APHIS) for providing the NRSS data and Karen Jamieson (Natural Resources Canada, Canadian Forest Service) for editing the manuscript. The participation of Denys Yemshanov was supported by an interdepartmental NRCAN - CFIA Forest Invasive Alien Species initiative. The participation of Mark Ducey was supported by the Agriculture and Food Research Initiative Competitive Grants Program Grant No. 2010-85605-20584 from the National Institute of Food and Agriculture.

References

- Andow DA, Kareiva PM, Levin SA, Okubo A (1990) Spread of invading organisms. *Landscape Ecology* 4: 177–188. doi: 10.1007/BF00132860
- APHIS (U.S. Department of Agriculture-Animal and Plant Health Inspection Service) (1999) APHIS Factsheet: invasive species. USDA APHIS, Riverdale, MD.
- APHIS (U.S. Department of Agriculture-Animal and Plant Health Inspection Service) (2010) The U.S. Department of Agriculture (USDA) seeks comments on National Firewood Task Force (NFTF) recommendations. http://www.aphis.usda.gov/publications/plant_health/content/printable_version/ia_firewood_taskforce.pdf
- APHIS (U.S. Department of Agriculture-Animal and Plant Health Inspection Service) (2011) Risk assessment of the movement of firewood within the United States. http://www.aphis.usda.gov/newsroom/hot_issues/firewood/downloads/firewood_pathway_assessment.pdf
- Arrow KJ (1971) Essays in the theory of risk-bearing. North-Holland: 1–278.
- Buchan LJ, Padilla DK (1999) Estimating the probability of long-distance overland dispersal of invading aquatic species. *Ecological Applications* 9: 254–265. doi: 10.1890/1051-0761(1999)009[0254:ETPOLD]2.0.CO;2
- CFIA (Canadian Food Inspection Agency) (2001) Plant Health Risk Assessment: Draft Guidelines for Commodity-specific Pest Risk Assessment. Plant Health Risk Assessment Unit, Nepean, ON.
- CFIA (Canadian Food Inspection Agency) (2012) Firewood – Don't Move Firewood. <http://www.inspection.gc.ca/english/plaveg/for/prod/firee.shtml#>

- Cook DC, Thomas MB, Cunningham SA, Anderson DL, De Barro PJ (2007) Predicting the economic impact of an invasive species on an ecosystem service. *Ecological Applications* 17: 1832–1840. doi: 10.1890/06-1632.1
- Environmental Systems Research Institute (ESRI) (2009) ESRI data & maps: 5-digit ZIP code points. Environmental Systems Research Institute, Redlands, CA.
- Fishburn PC, Vickson RC (1978) Theoretical foundations of stochastic dominance. In: Whittemore GA, Findlay MC (Eds) *Stochastic Dominance. An Approach to Decision-Making under Risk*. Lexington Books, D.C. Heath and Co., Lexington, MA, 39–144.
- Friedman M, Savage LJ (1948) The utility analysis of choices involving risk. *The Journal of Political Economy* 56(4): 279–304. doi: 10.1086/256692
- Gasbarro D, Wong W-K, Kenton ZJ (2009) Stochastic dominance and behaviour towards risk: The market for iShares. Social Science Research Network. doi: 10.2139/ssrn.1365756
- Gigerenzer G (2002) Calculated risks: How to know when numbers deceive you. Simon & Schuster, New York, NY.
- Goldberg DE (1989) Genetic algorithms in search, optimization, and machine learning. Addison-Wesley Publ. Co., Reading, MA, 1–412.
- Haack RA, Jendek E, Liu H, Marchant KR, Petrice TR, Poland TM, Ye H (2002) The emerald ash borer: a new exotic pest in North America. *Newsletter of the Michigan Entomological Society* 47(3–4): 1–5.
- Haack RA, Petrice TR, Wiedenhoff AC (2010) Incidence of bark- and wood-boring insects in firewood: a survey at Michigan's Mackinac Bridge. *Journal of Economic Entomology* 103: 1682–1692. doi: 10.1603/EC10041
- Hanoch G, Levy H (1969) The efficiency analysis of choices involving risk. *Review of Economic Studies* 36: 335–346. doi: 10.2307/2296431
- Hardaker JB, Richardson JW, Lien G, Schumann KD (2004) Stochastic efficiency analysis with risk aversion bounds: a simplified approach. *Australian Journal of Agricultural and Resource Economics* 48: 253–270. doi: 10.1111/j.1467-8489.2004.00239.x
- Hardaker JB, Lien G (2010) Stochastic efficiency analysis with risk aversion bounds: a comment. *Australian Journal of Agricultural and Resource Economics* 54: 379–383. doi: 10.1111/j.1467-8489.2010.00498.x
- Jacobi WR, Goodrich BA, Cleaver CM (2011) Firewood transport by national and state park campers: a risk for native or exotic tree pest movement. *Arboriculture & Urban Forestry* 37(3): 126–138.
- Kahneman D, Tversky A (1979) Prospect theory of decisions under risk. *Econometrica* 47(2): 263–291. doi: 10.2307/1914185
- Kahneman D, Slovic P, Tversky A (Eds) (1982) *Judgment under uncertainty: Heuristics and biases*. Cambridge University Press, New York, NY, 1–544.
- Koch FH, Yemshanov D, McKenney DW, Smith WD (2009) Evaluating critical uncertainty thresholds in a spatial model of forest pest invasion risk. *Risk Analysis* 29(9): 1227–1241. doi: 10.1111/j.1539-6924.2009.01251.x
- Koch FH, Yemshanov D, Magarey RD, Smith WD (2012) Dispersal of invasive forest insects via recreational firewood: a quantitative analysis. *Journal of Economic Entomology* 105(2): 438–450. doi: 10.1603/EC11270

- Kovacs KF, Haight RG, McCullough DG, Mercader RJ, Siegert NW, Liebhold AM (2010) Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. Ecological Economics 69: 569–578. doi: 10.1016/j.ecolecon.2009.09.004
- Lance DR (2003) APHIS (PPQ) exotic pest detection. In: Fosbroke SLC, Gottschalk KW (Eds) Proceedings, U.S. Department of Agriculture interagency research forum on gypsy moth and other invasive species 2002, 2002 January 15–18, Annapolis, MD. Gen. Tech. Rep. NE-300. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA, 54–55.
- Levy H (1992) Stochastic dominance and expected utility: survey and analysis. Management Science 38(4): 555–593. doi: 10.1287/mnsc.38.4.555
- Levy H (1998) Stochastic dominance: Investment decision making under uncertainty. Kluwer Academic Publishers, The Netherlands, 1–379.
- Levy M, Levy H (2001) Testing for risk aversion: A stochastic dominance approach. Economics Letters 71: 233–240. doi: 10.1016/S0165-1765(01)00377-9
- Magarey RD, Borchert DM, Engle JS, Colunga-Garcia M, Koch FH, Yemshanov D (2011) Risk maps for targeting exotic plant pest detection programs in the United States. EPPO Bulletin 41: 1–11. doi: 10.1111/j.1365-2338.2011.02437.x
- Markowitz H (1952) Portfolio selection. The Journal of Finance 7: 77–91.
- Melbourne BA, Hastings A (2009) Highly variable spread rates in replicated biological invasions: Fundamental limits to predictability. Science 325: 1536–1539. doi: 10.1126/science.1176138
- Meyer J (1977) Choice among distributions. Journal of Economic Theory 14: 326–336. doi: 10.1016/0022-0531(77)90134-X
- Meyer T, Xiao-Ming L, Rose LC (2005) Comparing mean variance tests with stochastic dominance tests when assessing international portfolio diversification benefits. Financial Services Review 14: 149–168.
- Meyer J, Richardson JW, Schumann KD (2009) Stochastic efficiency analysis with risk aversion bounds: a correction. Australian Journal of Agricultural and Resource Economics 53: 521–525. doi: 10.1111/j.1467-8489.2009.00471.x
- Muirhead JR, Leung B, van Overdijk C, Kelly DW, Nandakumar K, Marchant KR MacIsaac HJ (2006) Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. Diversity and Distributions 12: 71–79. doi: 10.1111/j.1366-9516.2006.00218.x
- NRCan (Natural Resources Canada) (2010) Geographical names digital products. Natural Resources Canada, Mapping Information Branch, Ottawa, ON. http://geonames.nrcan.gc.ca/prod/data_e.php
- 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. doi: 10.1890/08-1777.1
- Porter RB (1978) Portfolio applications: Empirical studies. In: Whitemore GA, Findlay MC (Eds) Stochastic dominance. An approach to decision-making under risk. Lexington Books, D.C. Heath and Co., Lexington, MA, 117–162.

- Porter RB, Wart JR, Ferguson L (1973) Efficient algorithms for conducting stochastic dominance tests on large numbers of portfolios. *Journal of Financial and Quantitative Analysis* 8: 71–81. doi: 10.2307/2329749
- Post T, Versijp P (2007) Multivariate tests for stochastic dominance efficiency of a given portfolio. *Journal of Financial and Quantitative Analysis* 42(2): 489–515. doi: 10.1017/S0022109000003367
- Post T (2003) Empirical tests for stochastic dominance efficiency. *Journal of Finance* 58: 1905–1931. doi: 10.1111/1540-6261.00592
- Rafoss T (2003) Spatial stochastic simulation offers potential as a quantitative method for pest risk analysis. *Risk Analysis* 23(4): 651–661. doi: 10.1111/1539-6924.00344
- Rothschild M, Stiglitz JE (1970) Increasing risk. I. A definition. *Journal of Economic Theory* 2: 225–243. doi: 10.1016/0022-0531(70)90038-4
- Schoemaker PJH (1982) The Expected Utility Model: Its variants, purposes, evidence and limitations. *Journal of Economic Literature* 20: 529–563.
- Shefrin H, Belotti ML (2007) Behavioural finance: biases, mean-variance returns, and risk premiums. In: CFA Institute Publications, June 2007, 4–12.
- Simberloff D (2005) The politics of assessing risk for biological invasions: the USA as a case study. *Trends in Ecology & Evolution* 20: 216–222. doi: 10.1016/j.tree.2005.02.008
- The Nature Conservancy (2011) Don't move firewood - trees and forests are threatened by invasive forest insects and diseases. <http://www.dontmovefirewood.org/>
- Tobin PC, Diss-Torrance A, Blackburn LM, Brown BD (2010) What does “local” firewood buy you? Managing the risk of invasive species introduction. *Journal of Economic Entomology* 103: 1569–1576. doi: 10.1603/EC10140
- Venette RC, Kriticos DJ, Magarey R, Koch FH, Baker RHA, Worner SP, Gómez NN, McKenney DW, Dobesberger EJ, Yemshanov D, De Barro PJ, Hutchison WD, Fowler G, Kalaris TM, Pedlar J (2010) Pest risk maps for invasive alien species: A roadmap for improvement. *BioScience* 60: 349–362. doi: 10.1525/bio.2010.60.5.5
- Whitemore GA, Findlay MC (1978) Introduction. In: Whitemore GA, Findlay MC (Eds) *Stochastic dominance. An approach to decision-making under risk*. Lexington Books, D.C. Heath and Co., Lexington, MA, 1–36.
- Yemshanov D, Koch FH, McKenney DW, Downing MC, Sapió 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. doi: 10.1111/j.1539-6924.2009.01203.x
- Yemshanov D, Koch FH, Ben-Haim Y, Smith WD (2010) Detection capacity, information gaps and the design of surveillance programs for invasive forest pests. *Journal of Environmental Management* 91: 2535–2546. doi: 10.1016/j.jenvman.2010.07.009
- Yemshanov D, Koch FH, Ducey M, Koehler K (2012a) Trade-associated pathways of alien forest insect entries in Canada. *Biological Invasions* 14: 797–812. doi: 10.1007/s10530-011-0117-5
- Yemshanov D, Koch FH, Lyons B, Ducey M, Koehler K (2012b) A dominance-based approach to map risks of ecological invasions in the presence of severe uncertainty. *Diversity and Distributions* 18: 33–46. doi: 10.1111/j.1472-4642.2011.00848.x

Appendix 1

Risk of out-of-state (out-of-province) locations to be the source of forest pests transported in firewood carried by campers. The risk rank values are based on the delineation of nested non-dominant sets via the first-degree stochastic dominance rule (FSD). The ranks close to 1.0 denote the highest risk of pest arrival and the ranks close to 0 denote the lowest risk. (doi: 10.3897/neobiota.18.4002.app1) File format: Adobe PDF File (pdf).

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Citation: Yemshanov D, Frank FH, Ducey MJ, Haack RA, Siltanen M, Wilson K (2013) Quantifying uncertainty in pest risk maps and assessments: adopting a risk-averse decision maker's perspective. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 193–218. doi: 10.3897/neobiota.18.4002 Risk of out-of-state (out-of-province) locations to be the source of forest pests transported in firewood carried by campers. doi: 10.3897/neobiota.18.4002.app1

Appendix 2

Risk of out-of-state (out-of-province) locations to be the source of forest pests transported in firewood carried by campers. The risk rank values are based on the delineation of nested non-dominant sets via the second-degree stochastic dominance rule (SSD), which embeds the notion of risk-averse decision choice. The ranks close to 1.0 denote the highest risk of pest arrival and the ranks close to 0 denote the lowest risk. (doi: 10.3897/neobiota.18.4002.app2) File format: Adobe PDF File (pdf).

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Citation: Yemshanov D, Frank FH, Ducey MJ, Haack RA, Siltanen M, Wilson K (2013) Quantifying uncertainty in pest risk maps and assessments: adopting a risk-averse decision maker's perspective. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 193–218. doi: 10.3897/neobiota.18.4002 Risk of out-of-state (out-of-province) locations to be the source of forest pests transported in firewood carried by campers. doi: 10.3897/neobiota.18.4002.app2

Appendix 3

Maps of differences in the risk ranks based on the first- and second-degree stochastic dominance rules, $\Delta r'_{ik} = r'_{ik \text{ FSD}} - r'_{ik \text{ SSD}}$. Positive values indicate that the FSD-based risk rank exceeds the SSD-based rank and vice versa. (doi: 10.3897/neobiota.18.4002. app3) File format: Adobe PDF File (pdf).

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Citation: Yemshanov D, Frank FH, Ducey MJ, Haack RA, Siltanen M, Wilson K (2013) Quantifying uncertainty in pest risk maps and assessments: adopting a risk-averse decision maker's perspective. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 193–218. doi: 10.3897/neobiota.18.4002 Maps of differences in the risk ranks based on the first- and second-degree stochastic dominance rules, $\Delta r'_{ik} = r'_{ik \text{ FSD}} - r'_{ik \text{ SSD}}$. doi: 10.3897/neobiota.18.4002.app3

Appendix 4

Summary of differences between risk rank classes, 0–0.05, 0.05–0.25, 0.25–0.5, 0.5–0.75, 0.75–0.95 and 0.95–1 in the delineations based on the FSD and SSD rules. (doi: 10.3897/neobiota.18.4002.app4) File format: Adobe PDF File (pdf).

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Citation: Yemshanov D, Frank FH, Ducey MJ, Haack RA, Siltanen M, Wilson K (2013) Quantifying uncertainty in pest risk maps and assessments: adopting a risk-averse decision maker's perspective. In: Kriticos DJ, Venette RC (Eds) Advancing risk assessment models to address climate change, economics and uncertainty. NeoBiota 18: 193–218. doi: 10.3897/neobiota.18.4002 Summary of differences between risk rank classes, 0–0.05, 0.05–0.25, 0.25–0.5, 0.5–0.75, 0.75–0.95 and 0.95–1 in the delineations based on the FSD and SSD rules. doi: 10.3897/neobiota.18.4002.app3
