

# Towards an integrated approach to modelling the risks and impacts of invasive forest species

Denys Yemshanov, Daniel W. McKenney, John H. Pedlar, Frank H. Koch, and David Cook

**Abstract:** In this paper we provide an overview of an integrated approach to modelling the risks and impacts associated with non-indigenous forest pest species. This is a broad and important topic given the scale of ecological and economic consequences associated with non-indigenous species in North America and elsewhere. Assessments of risks and impacts remain difficult due to complexities and interactions between the many factors driving invasions and outcomes. These processes occur across various spatial and temporal scales, and are often influenced and complicated by human activities. For each component of an ecological invasion (i.e., arrival, establishment, and spread), we review general approaches for modelling the phenomenon and identify data and knowledge gaps. With the greater availability of various spatial data and computational power we suggest the possibility of linking the models for each invasion component into a more integrated framework, thus allowing interactions and feedbacks between components to be better incorporated into risk modelling efforts. The approach is illustrated using examples from current work with *Sirex noctilio* Fabricius — a relatively new invasive wood wasp in eastern North America.

**Key words:** invasive species, integrated modelling, risk assessment, impact assessment, *Sirex noctilio*.

**Résumé :** Les auteurs présentent le survol d'une approche intégrée pour la modélisation des risques et des impacts associés aux pestes forestières non indigènes. Il s'agit d'un sujet large et important, compte tenu de l'échelle et des conséquences économiques associées aux espèces non indigènes, en Amérique du Nord et ailleurs. Les évaluations de risques et d'impacts demeurent difficiles à cause de la complexité et des interactions avec plusieurs facteurs responsables des invasions et de leurs conséquences. Ces processus s'effectuent selon différentes échelles spatio-temporelles, et sont souvent influencés et compliqués par les activités humaines. Pour chaque composante d'une invasion écologique (c.-à-d. arrivée, établissement et diffusion), les auteurs passent en revue les approches générales pour la modélisation du phénomène ainsi que l'identification des données et les manques de connaissance. Avec la disponibilité accrue de diverses données spatiales et des capacités informatiques, les auteurs suggèrent la possibilité de lier les modèles de chaque composante dans un cadre plus intégré, permettant ainsi de mieux incorporer les interactions et les rétroactions entre les composantes dans les efforts de modélisation des risques. On illustre cette approche en utilisant des exemples provenant du travail actuel sur le *Sirex noctilio* Fabricius, une guêpe perce-bois envahissante relativement nouvelle dans l'est de l'Amérique du Nord.

**Mots-clés :** espèces envahissantes, modélisation intégrée, évaluation des risques, évaluation des impacts, *Sirex noctilio*.

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## Introduction

The management of non-indigenous species is complex, but critical given potentially large economic and ecological

impacts. Gross annual economic losses and control costs in agricultural and forestry sectors due to non-indigenous species have been estimated to be greater than US\$110 billion in the USA (Pimentel et al. 2005) and greater than US\$7.5 billion in Canada (Dawson 2002). A similar estimate of the combined economic impact of non-indigenous species on agriculture and forestry in six countries (USA, UK, Australia, South Africa, India, and Brazil) exceeds US\$300 billion per year (Pimentel et al. 2001); this analysis further suggests the worldwide impact of non-indigenous species could exceed US\$1.4 trillion annually, or nearly 5% of the global domestic product. From an ecological perspective, non-indigenous species may alter the composition of native forest ecosystems and associated biodiversity (Merriam and Feil 2002). They may pressure, or even extirpate, species from large areas of their natural range (Latimer et al. 2004; Russell 1987), in some cases impacting forest foundation species such as the American chestnut (*Castanea dentata* (Marsh.) Borkh.) in the eastern USA or jarrah (*Eucalyptus marginata* Donn ex Sm.) in Western Australia (Ellison et al. 2005). Furthermore, new invaders may reduce recruit-

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**D. Yemshanov, D.W. McKenney,<sup>1</sup> and J.H. Pedlar.** Landscape Analysis and Applications Section, Canadian Forest Service, Great Lakes Forestry Centre, 1219 Queen Street E. Sault Ste. Marie, ON, P6A 5M7.

**F.H. Koch.** Department of Forestry and Environmental Resources, North Carolina State University. USDA Forest Service, Forest Health Monitoring Program, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA.

**D. Cook.** Commonwealth Scientific and Industrial Research Organization (CSIRO), Cooperative Research Centre for National Plant Biosecurity, Fenner School of Environment and Society, The Australian National University, GPO Box 1700, Canberra ACT 2601 Australia.

<sup>1</sup>Corresponding author (e-mail: dmckenne@NRCan.gc.ca).

ment rates and alter disturbance dynamics in natural ecosystems (Drake et al. 1989; Fagan and Peart 2004; Brooks et al. 2004).

The ongoing expansion of international trade is a key factor in this global-scale issue (Perrings et al. 2005), as a nation's non-indigenous species diversity is strongly related to its level of trade (Westphal et al. 2008). Not surprisingly, addressing the issue of exotic pests has become an important component of many trade and environmental policy agreements (Andersen et al. 2004a). Risk assessments for non-indigenous species are now standard procedure as prescribed by the World Trade Organization (WTO 1993). Nonetheless, far fewer countries mandate risk assessments for pests than for other environmental threats (e.g., pollutants), perhaps because the proportion of introduced species that actually become established pests is extremely low. As a rule of thumb, one in ten introduced species escapes into native environments, one in ten of these escapees establishes, and one in ten established species spreads in an invasive manner (Williamson 1996). Some introductions even provide economic benefits (Keller et al. 2007).

Whether or not pest risk assessments are standard practice, invasive species are constantly emerging that require quantitative evaluation of the risks and potential impacts involved (Levine and D'Antonio 2003). Because the economic and environmental consequences of a successful invader are irreversible (Saphores and Shogren 2005), management decisions are often made quickly out of apparent necessity, despite a paucity of reliable information about the invading organism. Moreover, most nations can only afford to collect limited data regarding the parameters of a biological invasion, meaning efficiency of effort is paramount (Saphores and Shogren 2005). These circumstances thus call for a strong but focused scientific foundation to support rapid assessments — ideally integrated with monitoring, mitigation, and even prevention efforts. These issues can be addressed with the aid of integrated modelling, which formalizes assumptions about the invading organism and uses them to quantify potential risks and impacts.

### The integrated modelling concept

There are numerous models focusing on certain aspects of biological invasions. For example, with respect to the initial, introduction phase of invasions, there have been regional- and global-scale efforts (Higgins et al. 1999; Davis and Pelsor 2001; Rouget and Richardson 2003; Thuiller et al. 2005) to identify geographic areas or ecosystems susceptible to successful introductions of non-indigenous species (i.e., which have high invasion likelihood), as well as attempts to predict which out of a set of species will be successful invaders (Veltman et al. 1996; Reichard and Hamilton 1997; Kolar and Lodge 2001; Frappier and Eckert 2003; Marchetti et al. 2004). Notably, few such studies have evaluated interactions between invasion potential and spread (Barney and Whitlow 2008). Other analyses have concentrated on later phases of invasions, for instance modelling the risk of establishment in new areas for recently detected non-indigenous species with still-restricted geographic distributions (e.g., Zalba et al. 2000; Morrison et al. 2004; Lippitt et al. 2008). In fact there are surprisingly few peer-reviewed studies of

the ex ante (potential) ecological (e.g., Ricciardi 2003) or economic impacts (e.g., Cook et al. 2007; Cook and Mathe-son 2008; Juliá et al. 2007) of individual invaders.

For specific species of concern, it is possible to quantify overall threats by aggregating and summarizing the outputs generated by individual specialized models (Pimentel et al. 2000; Allen and Humble 2002). However, this technique often misses the interactions and feedbacks between the various processes behind the invasion and may lead to miscalculation of the risks and impact projections. Alternatively, a more integrated modelling approach portrays an invasion as a simulation or optimization process that follows the typical flow of an exotic pest outbreak. This process starts with an introduction event as a result of trade and other human activities (Williamson 1996); once established in a new location, the invading organism spreads through the landscape causing host damage and mortality, which generates direct economic and environmental losses and triggers secondary social and economic impacts. All these processes occur under various geographical conditions and thus create intricate patterns in time and space (Fig. 1). Integrated models range in complexity from simple analytic approaches (e.g., Sharov and Liebhold 1998) to detailed, multi-phase mechanistic models driven by empirical data (such as Sharov and Colbert 1996). An appropriately integrated model should include both biophysical components (to simulate the impacts of the invading organism on a host resource), and non-biophysical aspects that estimate economic, social impacts, and other consequences.

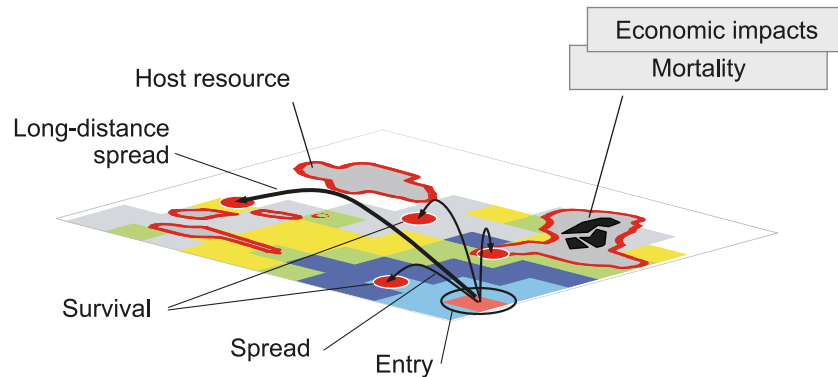
This paper provides an overview of an integrated modelling approach for non-indigenous species. For each of the key components of a biological invasion, we review pertinent literature, outline data and knowledge needs, and illustrate model results from our work with *Sirex noctilio* Fabricius, an invasive wood wasp recently discovered in eastern North America. In the final section, we discuss model integration and outline advantages of the integrated approach.

### Entry potential

The majority of non-indigenous species have been introduced to North America via transport of imported goods (Levine and D'Antonio 2003; Costello et al. 2007). This method of entry has become increasingly important as the volume of global trade has risen rapidly over the last decade: 7.4 billion tonnes in world seaborne trade in 2006, a 4.3% increase on the previous year (UNCTAD 2007). For decades, inspections at ports of entry have routinely detected unwanted organisms not just in cargoes but — particularly with respect to wood-boring insect pests — in their packaging as well (Brockerhoff et al. 2006; Haack 2006). This has prompted the recent development of stringent international phytosanitary standards for raw wood and wood packing materials (FAO-IPPC 2006).

For any given invading organism, an assessment of its entry potential can be seen as two separate analyses: identification of likely pathways for the invading organism to travel from countries of origin (Andersen et al. 2004b), and estimation of the entry potential at individual locations within the geographic area of interest (which may include

**Fig. 1.** The integrated modelling concept — showing the typical invasion process and resulting impacts. Gridded colors represent spatial heterogeneities associated with individual map locations in a two-dimensional landscape.



inland locations beyond initial ports of entry). The first analysis includes evaluation of the worldwide distribution of a species of concern, which permits identification of possible countries of origin (Magarey et al. 2007). It also includes assessment of likely import pathways, which can be accomplished by examining pest interception records as well as the status of commercial activities (e.g., timber production) with which the species is associated in origin countries (Baker et al. 2005; Magarey et al. 2007; Piel et al. 2008). The results may be used to establish a continuum of pest surveillance at ports of entry (Magarey et al. 2007). The second analysis focuses on pathways of imported goods after they enter at ports and evaluates the entry potential at final destination points (such as distribution centres and urban areas). Increasing volumes of container shipments and an ever-expanding transportation network in North America highlight a need for the evaluation of the flow of goods and commodities via major transportation corridors (Porojan 2001; De Jong et al. 2004; LeSage and Kelley Pace 2005; LeSage and Polasek 2006) and the volumes of intercity commodity transports (Black 1972; O'Sullivan and Ralston 1974).

Unfortunately, data relevant for calculating entry potential are often incomplete and inconsistent; for example, data for both domestic and international commodity flows omit certain trade sectors (Baker et al. 2005). One potential solution is to predict the entry potential at two levels: a global (i.e., broad-scale) likelihood of entry and a spatially explicit set of local entry probabilities that apportion the global entry potential into localized estimates for particular ports of entry (Herborg et al. 2007; Yemshanov et al. 2009b — see Fig. 2 for example with *S. noctilio*). This approach allows one to use separate data assumptions for global and local estimates and to test a wide range of local entry hypotheses independent of the global entry potential. For example, inland sites (such as distribution centres and urban areas) can be incorporated into the apportionment of entry potential among individual locations without changing the global entry potential. The approach also offers the opportunity to use more advanced transportation network and commodity flow models (similar to de Vos et al. 2004) to quantify the entry potential for a large, diverse set of locations.

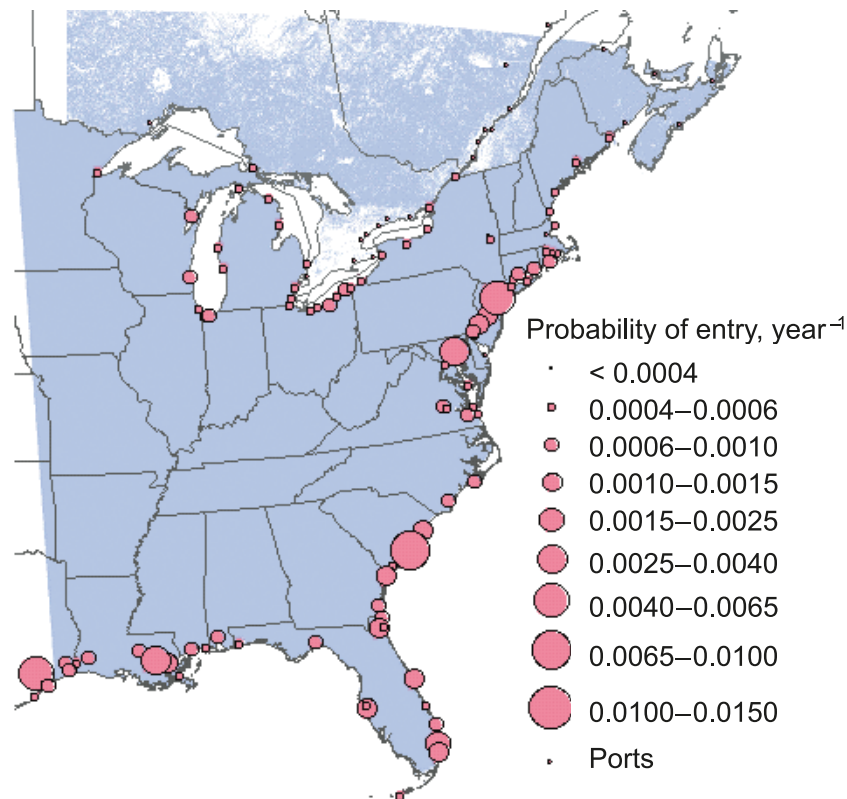
Several attempts have been made to assess the global entry potential of non-indigenous species at the continental level (McCullough et al. 2006; Ameden et al. 2007; Yem-

shanov et al. 2009b; also see Yamamura et al. 2001 for a national-scale example). Data available for such exercises include the total value of imports (e.g., Donnelly 2001 for USA and StatsCan (2008a, 2008b) for Canada), tonnages for specific marine import categories (e.g., USACE 2006 for USA and StatsCan (2003a, 2003b, 2004, 2005, 2007) for Canada) or proprietary databases such as USDA APHIS Port Information Network (PIN) interception records at ports of entry (McCullough et al. 2006) or USDA APHIS PPRIS database (Cohen et al. 1995). As depicted in the aforementioned examples, an analysis may be refined in a straightforward fashion by focusing only on commodity categories and countries of origin with which the species of interest has been previously associated.

Notably, entry potential is a dynamic variable that changes through time. Several studies have modelled global and local entry potential as a function of climate variables (Magarey et al. 2007), specific weather phenomena (such as El Niño), or certain socio-political and economic events such as the impact of new trade rules (Costello et al. 2007). Representing entry as a dynamic variable is likely more realistic than point-based techniques (Jarvis and Baker 2001) and also accounts for the possibility of multiple reintroductions over time (Rafoss 2003).

A number of recent studies have employed artificial neural network algorithms called self-organising maps (SOMs) to investigate entry and establishment potential of non-indigenous species based on cohabitation elsewhere in the world (Watts and Worner 2004; Gevrey and Worner 2006). Self-organising maps are used to project high dimensional global pest presence-absence data vectors onto a topological rectangular grid arranged as a hexagonal lattice (called a map) whilst preserving the similarities and differences between the data vectors (Gevrey et al. 2006). Establishment potential of each species is classified according to their weight of association to nodes within the map. The robustness of maps to changes in presence-absence status and dynamics of entry potential (i.e., changing trade environment, climate variability, etc.) is yet to be fully tested, but SOMs analysis has proved successful in investigating other complex ecological problems (e.g. Chon et al. 1996; Lek et al. 1996; Paruelo and Tomasel 1997; Lek and Guegan 1999; Giraudel et al. 2000; Brosse et al. 1999, 2001; Céréghino et al. 2001; Park et al. 2003).

**Fig. 2.** *Sirex noctilio* entry potential for major marine ports in eastern North America. The size of the circle indicates the probability of entry at each port.



## Spread

Whether a successfully introduced species is considered invasive rather than non-invasive in its new environment depends primarily on its ability to spread widely from the point(s) of entry (Kolar and Lodge 2001). Thus, it is not surprising that the spread of invading organisms remains one of the most intensively studied themes in ecological modelling (Royama 1992; Neubert and Caswell 2000; Okubo and Levin 2002; Nathan 2005). Two broad modelling approaches exist for forecasting the spread of non-indigenous species (Hastings 1996). The first approach employs theoretical analytic spread models such as reaction-diffusion traveling wave or stratified diffusion models (Shigesada et al. 1995; Kot et al. 1996; Sharov and Liebhold 1998) and uses field observation data to fit an analytic model to historical rates of spread (Holmes 1993). The analytic models are relatively simple and have been well studied (e.g., Royama 1992), but often lack feedbacks to biophysical and ecological factors. The approach also assumes that the future rate of spread will remain the same as the historical rate, which is not always true. There have been extensive studies to test this assumption against field data for a broad range of species (e.g.: Noble 1974; Lubina and Levin 1988; Yachi et al. 1989; Andow et al. 1993; Shigesada and Kawasaki 1997). In particular, failure to account for long-distance dispersal in analytical models has been a principal cause of underestimating true spread rates (Andow et al. 1990; Waage et al. 2005). Furthermore, observational data may simply be insufficient to characterize the rate of spread for a recent invader (Liebhold and Tobin 2008).

The second modelling approach incorporates detailed empirical information about the biology and behavior of the invading organism and relies on mechanistic (or process-based) algorithms that do not have analytic solutions; various ecological feedbacks may also be included (BenDor et al. 2006; Sharov and Colbert 1996). The parameter fitting procedures, however, often lack the transparency of analytic models and rely on expert knowledge about an invader — knowledge presumably gathered through research in the invader's previously known range. While these models may be seen as realistic with incorporation of species' life cycles and ecological preferences (Sharov and Colbert 1996), they can be difficult to validate and parameterize.

In general, spread models include at least three key components in various implementations (Neubert and Caswell 2000; Nathan 2005; BenDor et al. 2006): (1) population growth, (2) dispersal (or actual spread), and (3) establishment at newly colonized locations. Each of these components is reviewed below.

## Population growth

Ideally, modelling population growth proceeds from a thorough understanding of an invader's life cycle, climatic and environmental preferences, and other primary factors controlling its growth and mortality (Royama 1992). Life cycles, and interactions with host species, are being intensively studied for some new invaders (e.g., emerald ash borer, *Agrilus planipennis*, in North America: Bauer et al. 2003; Lyons et al. 2003), but are poorly understood in many cases (e.g., *S. noctilio*; Haugen and Hoebeke 2005).

Model development is often driven by data availability; species with more comprehensive geographic distribution records and life cycle details may be candidates for more detailed models (see discussion in Hastings et al. 2005). For some non-indigenous species, certain population model simplifications may be sidestepped by substituting characteristics from similar but better-understood species (see BenDor et al. 2006). Furthermore, extensive research on the population ecology of rare species, while undertaken largely for conservation purposes, has also proved instructive for modelling the early-stage population dynamics of non-indigenous species, which start with low population numbers as well (Liebhold and Tobin 2008). In short, reasonable models of population growth through time can be specified for many new invaders, albeit with some simplifying (yet testable) assumptions. Simplification is often driven by the apparent lack of observation records about new species but attempts to fit the population behavior to general knowledge about an invading organism or the data gathered in its native range.

### Dispersal

In generic terms, dispersal models link the positions of newly emerging individuals to the positions of their parents (van den Bosch et al. 1992). This can be depicted as a "dispersal kernel"  $K(x,y,z)$  that denotes the probability that an offspring from an individual born at location  $x$  at time  $z$  will start life at location  $y$ . In the general case, the kernel  $K$  can be defined as a probability density function (Neubert and Caswell 2000) for location  $y$  to which an individual at location  $x$  disperses. The probability density function  $K$  usually specifies how emerging adults spread to other locations. For example, in a simple one-dimensional case with a discrete time interval, the population density at the location  $x$  at time step  $t+1$  will be the sum of the contributions from all locations  $y$  with viable adults:

$$[1] \quad n(x, t + 1) = \int_{-\infty}^{+\infty} K(x, y, z) b[n(y, z, t), y] n(y, z, t) dy$$

where  $n(y,z,t)$  is population density at location  $y$  at age  $z$  and time  $t$ , and  $b[]$  is the net per capita population growth rate (Neubert and Caswell 2000). Various population growth models may be used to calculate  $b[]$  (see preceding section).

The shape of the probability density function  $K$  greatly affects the rate of spread and overall model behavior (Kot et al. 1996), but finding dispersal kernels that fit actual spread rates calculated from field observations can be challenging. The most basic kernel shape can be defined by a Gaussian probability-density function that produces a diffusion spread with constant velocity (Kot et al. 1996). However, several studies suggest that the Gaussian and other simple, commonly used kernels, such as the negative exponential, do not reflect the high proportional influence of long-distance dispersal that observational data on invasions often indicate (Chapman et al. 2007). For instance, an invasion's overall rate of spread accelerates if it proceeds from several nuclei (i.e., points of origin) at a given time step. This phenomenon can be portrayed by a two-tiered model of stratified diffusion (Shigesada et al. 1995) that adds a distance-dependent probability of creating new infection nuclei beyond the main front of the standard diffusion spread. Other ap-

proaches represent the long-distance dispersal as a spreading coalescing colony with a probability of creating new infection nuclei calculated as a function of the geographical distance from existing infestations (Sharov and Liebhold 1998).

Alternatively, a special group of "fat-tailed" probability density functions provides an increased probability of long-distance dispersal events and may be better able to simulate rapidly moving invasions (Clark et al. 1998; Chapman et al. 2007). Fat-tailed dispersal kernels also better capture two biological aspects of dispersal — heterogeneous movement (Skalski and Gilliam 2003) and habitat patchiness — which cause invading organisms to potentially cover long distances in search of new suitable locations (Morales 2002).

Although rare events of long-distance spread have been widely recognized as key contributors to the rates of migration (Clark et al. 1998; Nathan 2003), they are notoriously difficult to calibrate to real life outcomes (Andow et al. 1990; Shigesada and Kawasaki 1997, Higgins and Richardson 1999); the approaches described above offer only approximate solutions. A chief difficulty is that human activities also contribute to long-distance migration, but do not easily fit to "biological" models since they often depend on a variety of socioeconomic factors (e.g., the nature and extent of commercial or recreational opportunities at a given location). One way of predicting human-mediated, long-distance dispersal is through the use of "gravity" models (Bossenbroek et al. 2001). Gravity models relate the strength of interactions between invaded and non-invaded locations, weighted by the geographical distance between them, in a manner similar to a gravity law (Bossenbroek et al. 2001; Muirhead and MacIsaac 2005). These models assume that the migration of invading organisms is not strictly described by biological dispersal, but is biased by the "attractiveness" of potential destinations. Attractiveness (which denotes the degree of invasion potential) is usually based on various spatial and statistical assumptions about economic activities, infrastructure, and transportation routes (Muirhead et al. 2006). Despite their simplicity, gravity models may actually have better accuracy in predicting human-vectored organisms than theoretical dispersal models (Bossenbroek et al. 2001).

### Establishment

This phase refers to the period during which an invading organism grows and starts to reproduce in a recently colonized location. An establishment phase also occurs after an invasive species initially enters a region (see the section on entry potential), but here we present it as a component of spread in general. An invading organism requires certain resources to establish a new population in new locales, most obviously the presence of suitable hosts. Several studies have demonstrated the effect of host distribution on species spread rates (Turchin and Thoeny 1993; Durrett and Levin 1994; Shigesada and Kawasaki 1997; Weinberger 2002), population growth (Jules et al. 2002), and severity of impact of new invaders (Condeso and Meentemeyer 2007). Hovestadt et al. (2001) suggested that greater habitat (i.e., host) patch connectivity in invaded landscapes yields significant declines in dispersal mortality through time when compared with spatially homogeneous random landscapes. Kinezaki et al. (2003) showed that the degree of habitat fragmentation

changes an invader's global rate of spread (depending on the shape of the dispersal kernel used to characterize spread — see Weinberger 2002).

Spatially explicit maps of host occurrence or, more preferably, host abundance are required to successfully model where an invader is likely to establish in a functionally heterogeneous environment. For non-indigenous species that invade forested ecosystems, tree host species are typically of primary interest (although for some invasive pathogens such as *Phytophthora ramorum*, which causes sudden oak death, the distributions of shrub hosts may also be important). In North America, the distributions of tree species can be ascertained from a number of sources, including digital versions of Little's (Little 1971, 1976, 1977) tree range maps for the USA and national forest inventory data for both the USA (FIA, USDA Forest Service 2007) and Canada (Gillis 2001). For a wider range of species, a North American plant distribution database is also available (McKenney 2007a). National forest inventory data, generally collected on a network of plots, may be spatially interpolated or linked with medium-resolution satellite imagery (such as Landsat Thematic Mapper) through spatial randomization techniques to produce detailed, spatially continuous maps of tree species composition (Lowe et al. 2003; McRoberts et al. 2006; Yemshanov et al. 2009a). Figure 3 shows an example of a host distribution map of pine species, *Pinus* spp., constructed using these methods and used in the model of *S. noctilio* spread in eastern North America. It is also important to consider that host susceptibility may vary with age and stand conditions or between different host species (Paine and Millar 2002; Smith et al. 2002; Solla et al. 2005). Such cases can be managed in a spatially explicit model by linking age- and (or) species-dependent susceptibility assumptions to corresponding spatial data sources (maps of host resource) and thus adjusting the probability of successful invasion at any geographic location for a given time step. As with host species maps, maps of tree age and other stand attributes can be developed from National Forest Inventory data, however, this information usually has relatively poor spatial precision and high error levels because of difficulties in assessing and scaling up stand conditions and tree age from field sample plot observations.

At very broad spatial scales, the establishment potential of many non-indigenous species is ultimately constrained by climate (Stephenson 1990; Pearson and Dawson 2003). By identifying the climatic limits of an invading organism, unsuitable locations can be removed from the modelling process (see Fig. 4 for application to *S. noctilio*). Furthermore, mapping the climatic range provides a relatively quick estimate of the amount of land at risk; for this reason, such maps are often produced early in the risk assessment process to help guide initial response. Typically, generating such maps requires information on where the invading organism has historically been distributed (i.e., its presumed native range as well as any areas it invaded previously). This may be a very challenging prospect for some species and regions and, in many cases, distribution models must be generated from a handful of known occurrence locations. Fortunately, a great variety of analytical techniques have been developed for this purpose (see reviews in Elith et al. 2006; Kelly et al. 2007) and reasonable results can be obtained for most data-

sets. The climate data used in such analyses is readily available at both global (Hijmans et al. 2005) and continental (North American) scales (Magarey et al. 2007; McKenney 2007b).

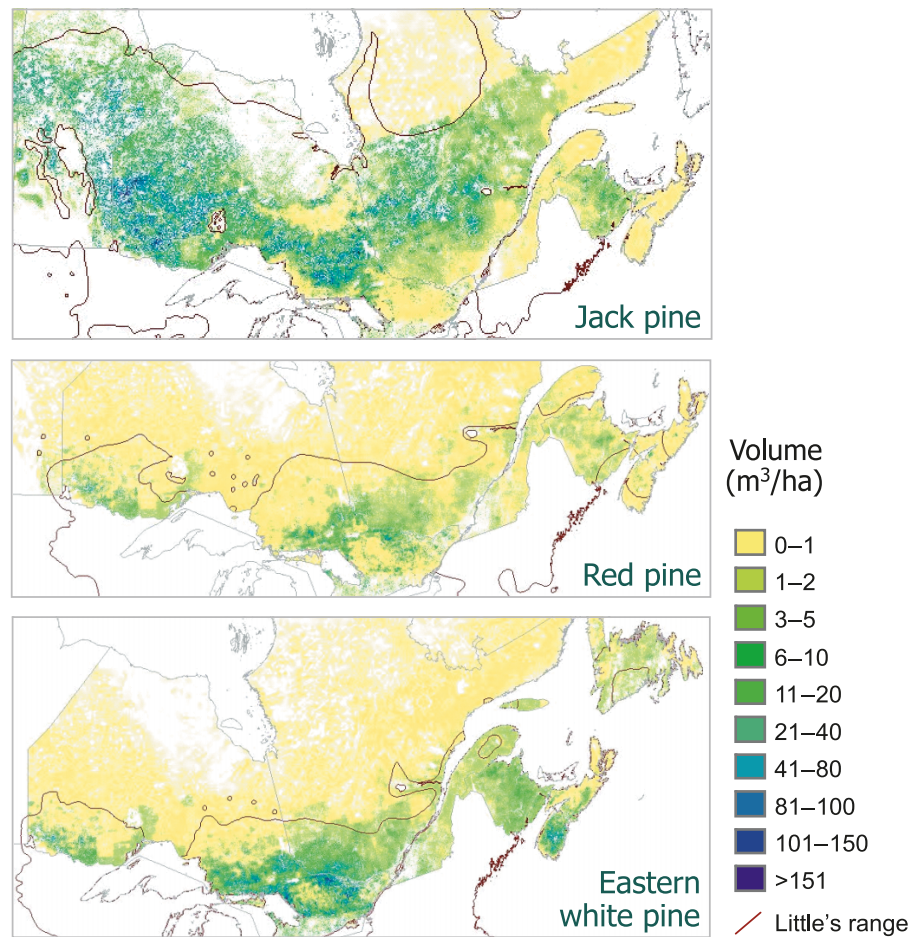
## Economic impacts

Economic impact analyses for non-indigenous species that attack plants often focus on direct losses in terms of reduced agricultural yield or biomass supply (e.g., Leeuwen et al. 2001; Borchert et al. 2007) as well as corresponding mitigation costs (such as removal and replacement of trees killed by the invading organism — see Sydnor et al. 2007). Cumulative costs (such as mill closures and associated job losses) and non-market costs (such as loss of biodiversity) are more difficult to quantify (Leung et al. 2002; Keller et al. 2007). Existing broad-scale estimates of the total annual costs of non-indigenous species (e.g., US OTA 1993; Pimentel et al. 2001, 2005) raise awareness about the problem's scope, but do little to support more managerial responses.

Ultimately, more detailed economic analyses are necessary to fully assess the costs and benefits associated with various management strategies and identify those that are most cost-effective (Perrings et al. 2000; Leung et al. 2005; Cook et al. 2006). Decision makers have a number of options for control after an invading organism arrives in a new locale, including eradication, containment (for example, through regulations imposed on movement of potentially infected materials), "slow-the-spread" efforts, and introduction of biological control agents. In general, decision analyses for non-indigenous species rely on the basic optimal resource management concept (see Clark 1990), where the objective is to maximize the discounted sum of social welfare provided by a biological resource (Nyarko and Olson 1991; Olson and Roy 1996, 2002). Published studies have, for example, estimated the costs and benefits of specific control strategies (Cacho 2005; Cook et al. 2006), analyzed the trade-offs between eradication and slow-the-spread programs (Sharov and Liebhold 1998; Sharov et al. 1998), evaluated the relative cost-effectiveness of control strategies targeted towards particular life stages of an invading organism (Buhle et al. 2005), and used conflict resolution analysis to choose between alternative control strategies (Higgins et al. 1997). Notably, economic analyses regarding eradication measures are rare, perhaps because many non-indigenous species remain undetected until reasonably well established, making eradication a failure-prone and prohibitively expensive option (Born et al. 2005; Fraser et al. 2006).

Assessing the economic impact of imposing regulatory policies is a more complex task, given that outbreaks usually cover large areas with a mix of urban, rural, and natural settings. While there have been some broad-scale, conceptual analyses of the impacts of trade regulations on non-indigenous species introduction risk (e.g., McAusland and Costello 2004; Cook and Fraser 2008), there have been few specific case studies that have considered regulatory efforts at least in part. Noteworthy examples include a comparison of the costs for different strategies for preventing a potential *Chrysomya bezziana* Villeneuve outbreak in Australia (Anaman et al. 1994), costs of eradication of aquatic species (Cacho 2005), costs of eradication of Karnal bunt in Aus-

**Fig. 3.** Distribution and abundance of three species of *Pinus* that act as hosts for *Sirex noctilio*. Abundance estimates were obtained by linking coarse-scale national forest inventory data with medium-resolution satellite imagery through a spatial randomization technique. The brown lines indicate Little's (Little 1971) range map for each species.



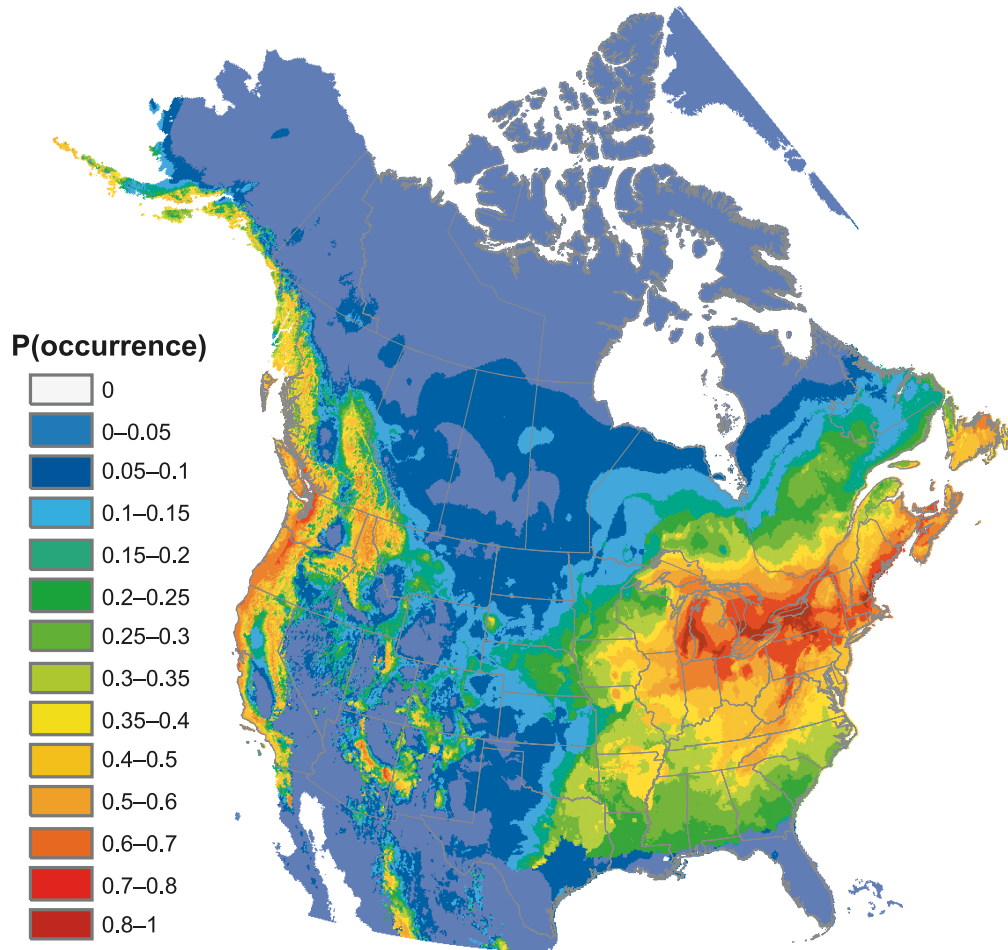
tralia (Wittwer et al. 2005), damages from the zebra mussel in North America (Khalanski 1997), and the costs of prevention and control policies (Leung et al. 2002). Similarly, few studies have assessed the costs of biological control programs (see review in Hill and Greathead 2000). The results include cost-benefit ratios that vary by three orders of magnitude. Programs with the highest cost-benefit ratios usually cover large geographic areas and target economically important species (Hill and Greathead 2000).

The reason for this wide variation in program costs is the tremendous uncertainty in the structure of the aggregate costs of invasion, in turn eroding confidence in predictive model results. In response to this problem several formal economic frameworks for risk management have been proposed. These use a variety of methods, including risk-based models (Shogren 2000), stochastic dynamic programming (Eiswerth and van Kooten 2002), and hierarchical Bayesian statistics (Rinella and Luschei 2007). These prediction-based techniques relying on expected utility maximization are of limited value when no information exists on which to base either invasion scenarios or their probabilities of occurrence. In such circumstances alternative policy decision rules have been devised, such as the minimax criterion where policies are formed to minimize social losses in a worst-case sce-

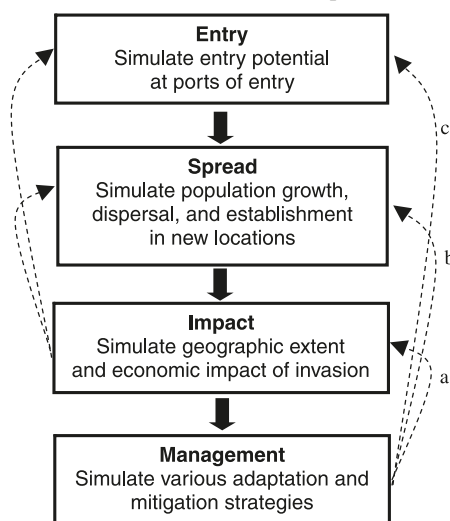
nario (Moffitt and Osteen 2006). Essentially the worst-case scenario is based on Wald's maximum model of uncertainty (Wald 1945) that uses the worst-case outcomes as a hedge against severe uncertainty in model assumptions and data. More sophisticated decision rules are presented in Horan et al. (2002) and Moffitt et al. (2006).

The uncertainty surrounding non-indigenous species makes contingency planning difficult, thus creating great demand for ex ante impact assessments (Perrings et al. 2000; Raghu et al. 2007). It is a challenge to execute detailed economic impact analyses for large-scale heterogeneous environments, since blanket policies for non-indigenous species may have quite different consequences in different locales (Leung et al. 2002). Often when very little is known about a new invader, an impact assessment may simply identify the gross potential amount of host resource under threat and multiply this quantity by some unit price (Borchert et al. 2007). This technique is very popular in impact assessments of exotic forest pests; however it does not address important issues such as when and where invasion-induced wood supply shortages might occur or equating the marginal benefits of management decisions with the marginal costs as would be the case in a more economically oriented approach (Fox et al. 1997). The latter is a more complex problem and re-

**Fig. 4.** Climatic suitability map for *Sirex noctilio* showing the occurrence probability ( $P_{(\text{occurrence})}$ ) based on a maximum entropy interpolation (Phillips et al. 2006) of the worldwide *S. noctilio* occurrence data shown in Carnegie et al. (2006). The climate variables used in the model included: annual mean temperature, average minimum temperature of the coldest month, average maximum temperature of the hottest month, annual precipitation, precipitation of the coldest month, and precipitation of the hottest month.



**Fig. 5.** Major components of the integrated modelling approach. Feedbacks are shown with dashed lines. Management initiatives can be applied at various points in the invasion process and may include activities such as: (a) salvage logging; (b) slow-the-spread programs; and (c) increased surveillance at points of entry.

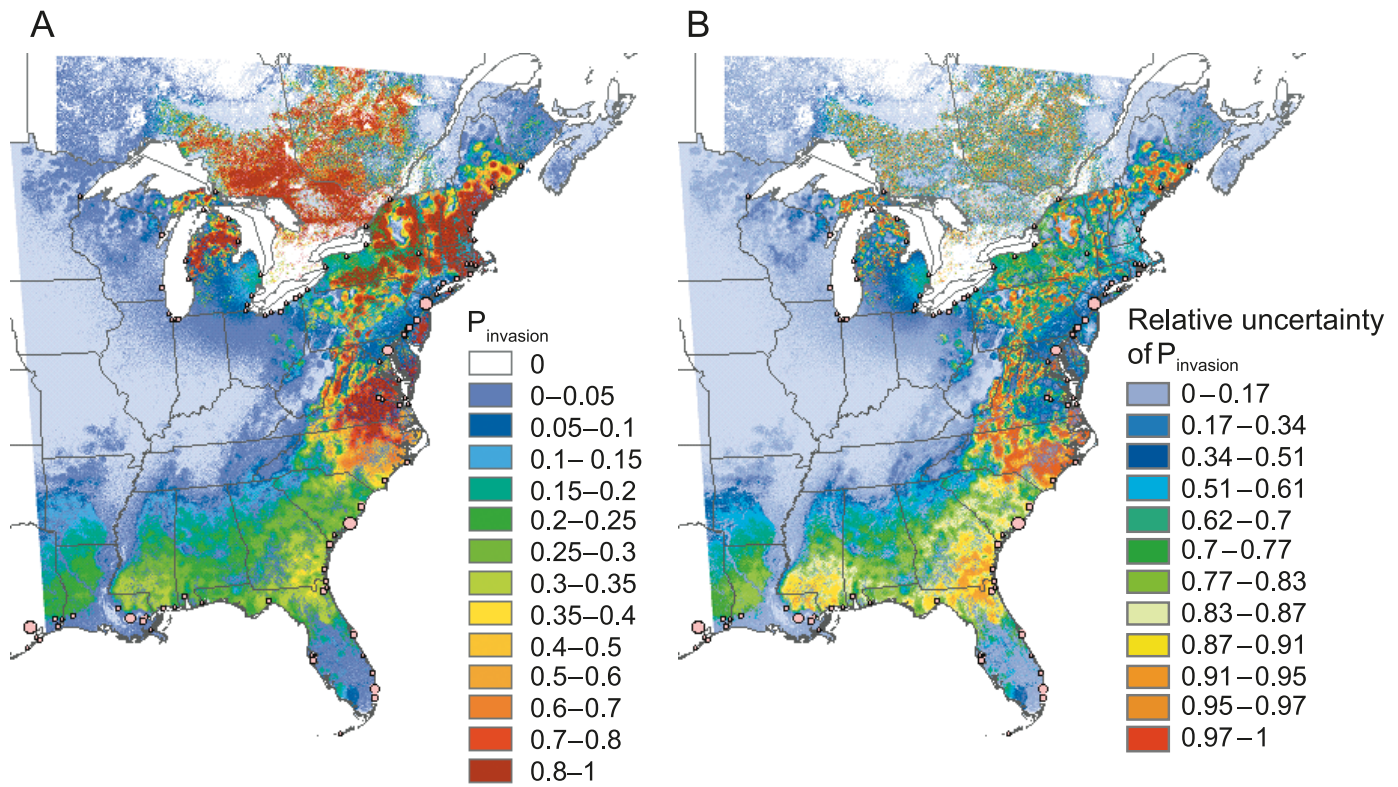


quires linking the invasion model with the use and management of forest resources. Impact assessments on commercial wood supply must also account for existing forest management practices and regulatory guidelines that may be restricted to certain administrative and political boundaries.

When implemented in a spatial setting, integrated models can or should recreate the heterogeneous nature of natural landscapes, host distribution and pathways of introduction and spread of invading organisms hence offering a more accurate representation of potential damages to a host resource (and thus a more accurate representation of economic impacts). Furthermore, the approach can be linked with existing forest management models such as harvest and wood supply allocation programs (Weintraub and Navon 1976; Bettinger et al. 2002; Peter and Nelson 2005) hence better representing the dynamic nature of major forest management activities. For example, Yemshanov et al. (2009a) provided geographically referenced depictions of the potential impacts of the *S. noctilio* invasion to wood supply markets in eastern Canada. By integrating the spread model with a harvest allocation model, they identified major areas of potential wood supply shortages, associated direct economic losses and effectiveness of potential harvest adaptation policies. The



**Fig. 6.** Risk and uncertainty maps, (*Sirex noctilio*, 30-year time horizon) showing: (a) probability of invasion,  $P_{\text{invasion}}$ ; and (b) relative uncertainty of  $P_{\text{invasion}}$  (shown here as a binary entropy metric). A technical description of the risk mapping methodology can be found in Yemshanov et al. (2009b).



study suggested that adaptation policies could decrease short-term losses by 46%–55% and help delay larger wood supply failures by up to 9–11 years.

### Benefits of integration

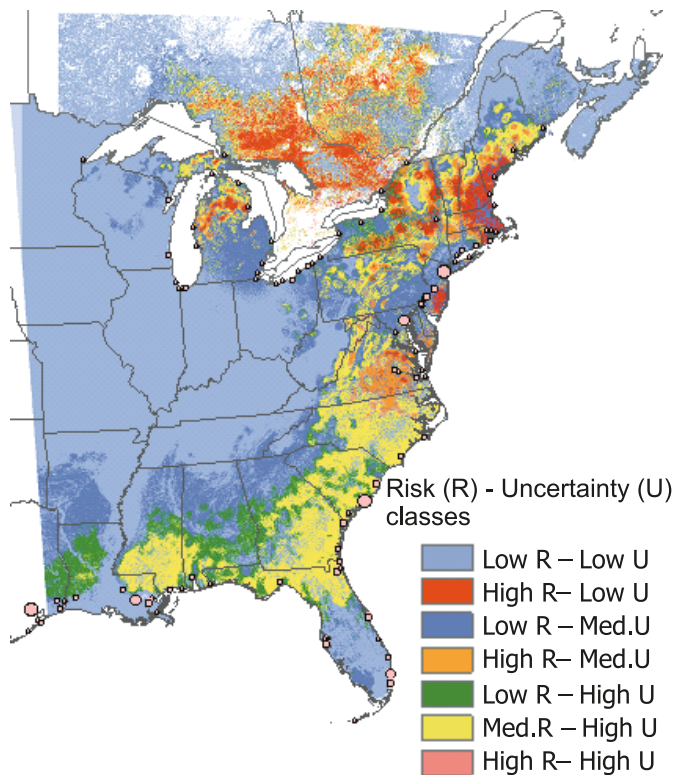
Given the potentially significant economic ramifications, any decision about managing non-indigenous species should be based on the best available biological and ecological knowledge about the invading organism (Fox et al. 1997). We suggest that this objective can be better addressed by combining biophysical and economic components into a single integrated modelling framework. A unique characteristic of an integrated "bioeconomic" approach is the ability to incorporate feedbacks between the biophysical, economic, and policy components of one model (Finnoff et al. 2005). For example, the "biological" model components generate spread projections of an invading organism and its impact on a host resource. Impact caused by host mortality subsequently affects the future spread potential of an invading organism. The "economic" modules then use these outputs for real-time tracking of the damage costs and impacts on "business-as-usual" activities. In turn, economic outcomes and various mitigation strategies (such as quarantine or slow-the-spread protocols) can be linked back to the biophysical components to evaluate their real costs and effectiveness (Fig. 5).

The integrated modelling approach has a number of other advantages. First, integrating the model in a spatial setting offers the capacity of representing actual geographic variation of key biophysical and economic drivers. In fact, entry

and spread are spatial processes per se and thus fit naturally into a geographic framework. Spread, risk, and impact estimates can be generated at broad spatial scales with adequate accuracy to outline geographic hotspots while still providing a larger context for the problem (see Fig. 6a for example). Second, integrated models may better estimate the cumulative impacts and spatial dependencies that might occur as a result of multiple introductions. This becomes especially valuable for assessing complex situations, including both the existing and potential infestations scattered across large and diverse geographical regions (Rafoss 2003; Yemshanov et al. 2009b). Third, sensitivity analyses can be employed to help reveal the relative importance of key features of the invading organism (e.g., entry potential, population growth rate, dispersal distances or host susceptibility) and their impact on particular model outputs (Neubert and Caswell 2000; Watkinson et al. 2000). Sensitivity analyses also help identify key drivers behind the invasion and potential knowledge gaps, which may lead to insights on how to control or eradicate the species (Watkinson et al. 2000). This is an important point as many invasive species have no prior observations in North America, making their risk potential highly uncertain.

Finally, a stochastic implementation offers a way to estimate the uncertainty of invasion in a manner useful to decision makers. While widely acknowledged as a problem, uncertainty can be a challenge to quantify, especially for geographically explicit analyses. As a result, uncertainties are often omitted from risk modelling efforts, so outputs convey more confidence than actually exists (Woodbury

**Fig. 7.** Risk–uncertainty map for *Sirex noctilio* based on a 30-year time horizon with risk–uncertainty classes shown in the legend ( $R$  = risk,  $U$  = uncertainty). A technical description of the risk–uncertainty classification can be found in Yemshanov et al. (2009b).



2003; Meentemeyer et al. 2004; FHTET 2007). Integrated models provide means of identifying and discriminating particular sources of uncertainty (such as natural variability or input data errors; Regan et al. 2002; Elith et al. 2002). For example, multiple stochastic model replications can be used to build probabilistic maps of invasion risks and uncertainties for a given time horizon and region of interest (Yemshanov et al. 2009b; Fig. 6b). A simple classification of the risks and uncertainties combined in a single map (Fig. 7) can then serve as a practical guide for decision makers.

In fact, several general techniques have been proposed to quantify uncertainties, with sensitivity analysis among the most widely used (Morgan and Henrion 1990). Sensitivity analysis involves systematic alteration of model parameter (or input) values to observe their relative effects on a target output variable (Swartzman and Kaluzny 1987; Walley 1991; Henderson-Sellers and Henderson-Sellers 1996), and usually quantifies uncertainty using a standard probability model. Ensemble prediction systems (Worner and Gevrey 2006; Demeritt et al. 2007) that combine the forecasts made with different models represent another alternative, addressing, at least in part, uncertainty due to model structure or formulation (Buizza et al. 2005, Araújo and New 2007). Several other approaches attempted to solve the issue of uncertainties through multi-criteria decision analysis and valuation (Keeney and Raiffa 1976; von Winterfeldt and Edwards 1986; Stewart 1992). The general idea of these ef-

forts is to translate vague objectives into more precise performance indicators.

Although there are many advantages to the integrated approach, there are of course several potential drawbacks. Gathering the volume of information needed to model the entire invasion process — complete with economic impacts and management scenarios — can be daunting and may be beyond the scope of many research programs. Furthermore, the large number of inputs means there are also many opportunities for error; by combining the models for each invasion component, errors may get multiplied, making the final outputs highly prone to error. There is no simple solution to this situation, model outputs will only be as good as the data that goes into the model and thus it is essential that each component of an integrated model is parameterized as accurately as possible. A final consideration is that of validating the results from an integrated modelling effort. Finding independent validation data for current invasive threats is extremely challenging since the invasion process is often in a relatively early stage of advance, and any spatial occurrence data that is available is often used in model development. Furthermore, such models are often oriented around assessing *potential* as opposed to actual outcomes; this makes model validation problematic and somewhat irrelevant. Nevertheless, one possible approach could be to model the potential spread of a long-established invasive species and then test model predictions against actual spread data obtained from historical occurrence records for that species (see Higgins et al. 2001). Though this method can only be used for invasive species with a long history in an area, positive results should lend confidence to model predictions for more contemporary invasive threats.

## Concluding comments

Non-indigenous species can be major economic and biological threats and they remain a major challenge for decision makers. Often, generating defensible assumptions about how an invading organism will behave in a new environment is extremely difficult, thus decisions have to be made under tenuous assumptions based on little a priori knowledge. Integrated bioeconomic models offer a particularly promising approach for assessing aggregate risks of non-indigenous species.

Our review indicates that there is a growing base of theoretical knowledge and data to support practical integrated modelling initiatives for non-indigenous species. Entry potential can be modelled using marine import data to define global and port-specific probabilities of entry. Spread models can incorporate both well-defined spread dynamics equations and expert knowledge into estimates of population growth, dispersal, and establishment of invading organisms. Outputs, in terms of host resource losses, can then be assessed for economic value and mitigation options using standard cost-benefit analyses but in a context that should be more useful to practical decision-makers.

Integrated risk assessments will benefit from further work in a number of areas. Basic information, such as host distribution and abundance, can be very difficult to obtain for many species and locations. Similarly, reliable information on the distribution of non-indigenous species in their coun-

try of origin is usually scarce, making it difficult to define the climatic tolerances of an invading species. Ongoing data collection will also be needed to generate species-specific spread parameters and to better understand the phenomenon of rare, long-distance dispersal events. Despite these limitations, our experience suggests that the data and knowledge are increasingly in place to generate informative, testable integrated risk assessments for many non-indigenous species.

## References

- Allen, E.A., and Humble, L.M. 2002. Nonindigenous species introductions: a threat to Canada's forests and forest economy. *Can. J. Plant Pathol.* **24**: 103–110.
- Ameden, H., Cash, S.B., and Zilberman, D. 2007. Border enforcement and firm response in the management of invasive species. *J. Agric. Applied Econ.* **39**: 35–46.
- Anaman, K.A., Atzeni, M.G., Mayer, D.G., and Walthall, J.C. 1994. Economic assessment of preparedness strategies to prevent the introduction or the permanent establishment of screw worm fly in Australia. *Prev. Vet. Med.* **20**(1-2): 99–111. doi:10.1016/0167-5877(94)90110-4.
- Andersen, M.C., Adams, H., Hope, B., and Powell, M. 2004a. Risk assessment for invasive species. *Risk Anal.* **24**(4): 787–793. doi:10.1111/j.0272-4332.2004.00478.x. PMID:15357799.
- Andersen, M.C., Adams, H., Hope, B., and Powell, M. 2004b. Risk analysis for invasive species: general framework and research needs. *Risk Anal.* **24**(4): 893–900. doi:10.1111/j.0272-4332.2004.00487.x. PMID:15357808.
- Andow, D., Kareiva, P., Levin, S., and Okubo, A. 1990. Spread of invading organisms. *Landsc. Ecol.* **4**(2-3): 177–188. doi:10.1007/BF00132860.
- Andow, D., Kareiva, P., Levin, S., and Okubo, A. 1993. Spread of invading organisms: patterns of spread. *In Evolution of insect pests: the pattern of variations. Edited by K. Kim.* Wiley, New York, USA. pp. 219–242.
- Araújo, M.B., and New, M. 2007. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* **22**(1): 42–47. doi:10.1016/j.tree.2006.09.010. PMID:17011070.
- Baker, R., Cannon, R., Bartlett, P., and Barker, I. 2005. Novel strategies for assessing and managing the risks posed by invasive alien species to global crop production and biodiversity. *Ann. Appl. Biol.* **146**(2): 177–191. doi:10.1111/j.1744-7348.2005.040071.x.
- Barney, J.N., and Whitlow, T.H. 2008. A unifying framework for biological invasions: the state factor model. *Biol. Invasions*, **10**(3): 259–272. doi:10.1007/s10530-007-9127-8.
- Bauer, L.S., Haack, R.A., Miller, D.L., Petrice, T.T., and Liu, H. 2003. Emerald ash borer life cycle. *In Abstracts of Emerald Ash Borer Research and Technology Development Meeting. Edited by V. Mastro and R. Reardon.* Report: USDA FHTET 2004-02. Forest Health Technology Enterprise Team.
- BenDor, T.K., Metcalf, S.S., Fontenot, L.E., Sangunett, B., and Hannon, B. 2006. Modelling the spread of the Emerald Ash Borer. *Ecol. Model.* **197**(1-2): 221–236. doi:10.1016/j.ecolmodel.2006.03.003.
- Bettinger, P., Graetz, D., Boston, K., Sessions, J., and Chung, W. 2002. Eight heuristic planning techniques applied to three increasingly difficult wildlife planning problems. *Silva Fenn.* **36**: 561–584.
- Black, W.R. 1972. Interregional commodity flows: some experiments with the gravity model. *J. Reg. Sci.* **12**(1): 107–118. doi:10.1111/j.1467-9787.1972.tb00282.x.
- Borchert, D., Fowler, G., and Jackson, L. 2007. Organism pest risk analysis: risks to the conterminous United States associated with the woodwasp, *Sirex noctilio* Fabricius, and the symbiotic fungus, *Amylostereum areolatum*, (Fries: Fries) Boidin. USDA-APHIS-PPQ-CPHST-PERAL. Rev.1. Available from www.aphis.usda.gov/plant\_health/plant\_pest\_info/sirex/downloads/sirex-pra.pdf [accessed March 2009].
- Born, W., Rauschmayer, F., and Bräuer, I. 2005. Economic evaluation of biological invasions – a survey. *Ecol. Econ.* **55**(3): 321–336. doi:10.1016/j.ecolecon.2005.08.014.
- Bossenbroek, J.M., Kraft, C.E., and Nekola, J.C. 2001. Prediction of long-distance dispersal using gravity models: zebra mussel invasion of inland lakes. *Ecol. Appl.* **11**(6): 1778–1788. doi:10.1890/1051-0761(2001)011[1778:POLDDU]2.0.CO;2.
- Brockhoff, E.G., Bain, J., Kimberley, M., and Knížek, M. 2006. Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. *Can. J. For. Res.* **36**: 289–298. doi:10.1139/x05-250.
- Brooks, L.M., Dantonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.B., Di Tomaso, J.M., Hobbs, R.J., Pellant, M., and Pyke, D. 2004. Effects of invasive alien plants on fire regimes. *Bioscience*, **54**(7): 677–688. doi:10.1641/0006-3568(2004)054[0677:EOIAPQ]2.0.CO;2.
- Brosse, S., Guegan, J.-F., Tourenq, J.-N., and Lek, S. 1999. The use of artificial neural networks to assess fish abundance and spatial occupancy in the littoral zone of a mesotrophic lake. *Ecol. Model.* **120**(2-3): 299–311. doi:10.1016/S0304-3800(99)00110-6.
- Brosse, S., Giraudel, J.L., and Lek, S. 2001. Utilisation of non-supervised neural networks and principal component analysis to study fish assemblages. *Ecol. Model.* **146**(1-3): 159–166. doi:10.1016/S0304-3800(01)00303-9.
- Buhle, E.R., Margolis, M., and Ruesink, J.L. 2005. Bang for buck: cost-effective control of invasive species with different life histories. *Ecol. Econ.* **52**: 355–366.
- Buizza, R., Houtekamer, P.L., Toth, Z., Pellerin, G., Wei, M., and Zhu, Y. 2005. A comparison of the ECMWF, MSC, and NCEP global ensemble prediction systems. *Mon. Weather Rev.* **133**(5): 1076–1097. doi:10.1175/MWR2905.1.
- Cacho, O. 2005. Invasive species in aquatic ecosystems: economics and matrix population models. Working Paper Series in Agricultural Resource Economics. No. 2005-5. University of New England, Armidale, Australia.
- Carnegie, A.J., Matsuki, M., Haugen, D.A., Hurley, B.P., Ahumada, R., Klasmer, P., Sun, J., and Iede, E.T. 2006. Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of *Pinus* plantations. *Ann. For. Sci.* **63**(2): 119–128. doi:10.1051/forest:2005104.
- Céréghino, R., Giraudel, J.L., and Compin, A. 2001. Spatial analysis of stream invertebrates distribution in the Adour-Garonne drainage basin (France), using Kohonen self organizing maps. *Ecol. Model.* **146**(1-3): 167–180. doi:10.1016/S0304-3800(01)00304-0.
- Chapman, D.S., Dytham, C., and Oxford, G.S. 2007. Modelling population redistribution in a leaf beetle: an evaluation of alternative dispersal functions. *J. Anim. Ecol.* **76**(1): 36–44. doi:10.1111/j.1365-2656.2006.01172.x. PMID:17184351.
- Chon, T.S., Park, Y.S., Moon, K.H., and Cha, E.Y. 1996. Patternizing communities by using an artificial neural network. *Ecol. Model.* **90**(1): 69–78. doi:10.1016/0304-3800(95)00148-4.
- Clark, C.W. 1990. Mathematical bioeconomics: the optimal management of renewable resources. 2nd ed. John Wiley & Sons, New York.
- Clark, J.S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King,

- G.A., Lewis, M.A., Lynch, J., Pacala, S., Prentice, C., Schupp, E.W., Webb, T., III, and Wyckoff, P. 1998. Reid's paradox of rapid plant migration: dispersal pattern and interpretation of paleoecological records. *Bioscience*, **48**: 13–24.
- Cohen, S.D., Chang, L.W., Griffin, R.L., and Orr, R.L. 1995. Plant pest risk information system (PPRIS) for USDA-APHIS: design of a functional prototype. *EPPO Bulletin*, **25**(4): 637–650. doi:10.1111/j.1365-2338.1995.tb01116.x.
- Condeso, T.E., and Meentemeyer, R.K. 2007. Effects of landscape heterogeneity on the emerging forest disease sudden oak death. *J. Ecol.* **95**(2): 364–375. doi:10.1111/j.1365-2745.2006.01206.x.
- Cook, D.C., and Fraser, R.W. 2008. Trade and invasive species risk mitigation: Reconciling WTO compliance with maximising the gains from trade. *Food Policy*, **33**(2): 176–184. doi:10.1016/j.foodpol.2007.07.001.
- Cook, D.C., and Matheson, A.C. 2008. An estimate of the potential economic impact of pine pitch canker in Australia. *Australian Forestry*, **71**: 107–112.
- Cook, D.C., Waage, J.K., Mumford, J.D., Fraser, R.W., and Wilby, A. 2006. T8.11: The benefits of potato ring rot exclusion from the United Kingdom. Office of Science and Innovation, Department of Trade and Industry, UK. Available from [www.foresight.gov.uk/Infectious%20Diseases/t8\\_11.pdf](http://www.foresight.gov.uk/Infectious%20Diseases/t8_11.pdf) [accessed March 2009].
- Cook, D.C., Thomas, M.B., Cunningham, S.A., Anderson, D.L., and De Barro, P.J. 2007. Predicting the economic impact of an invasive species on an ecosystem service. *Ecol. Appl.* **17**(6): 1832–1840. doi:10.1890/06-1632.1. PMID:17913144.
- Costello, C., Springborn, M., McAusland, C., and Solow, A. 2007. Unintended biological invasions: does risk vary by trading partner? *J. Environ. Econ. Manage.* **54**(3): 262–276. doi:10.1016/j.jeem.2007.06.001.
- Davis, M.A., and Pelsor, M. 2001. Experimental support for a resource-based mechanistic model of invasibility. *Ecol. Lett.* **4**(5): 421–428. doi:10.1046/j.1461-0248.2001.00246.x.
- Dawson, M. 2002. Plant quarantine: a tool for preventing the introduction and spread of alien species harmful to plants. *In Alien Invaders in Canada's Waters, Wetlands and Forests. Edited by R. Claudi, P. Nantel, and E. Muckle-Jeffs.* Canadian Forest Service, Ottawa, Ont. pp. 243–251.
- De Jong, G., Gunn, H.F., and Walker, W. 2004. National and international freight transportation models: an overview and ideas for further developments. *Transp. Rev.* **24**: 103–124.
- Demeritt, D., Cloke, H., Pappenberger, F., Thielen, J., Bartholmes, J., and Ramos, M. 2007. Ensemble predictions and perceptions of risks, uncertainty, and error in flood forecasting. *Environmental Hazards*, **7**(2): 115–127. doi:10.1016/j.envhaz.2007.05.001.
- de Vos, C.J., Saatkamp, H.W., Nielen, M., and Huirne, R.B.M. 2004. Scenario tree modeling to analyze the probability of classical swine fever virus introduction into member states of the European Union. *Risk Anal.* **24**(1): 237–253. doi:10.1111/j.0272-4332.2004.00426.x. PMID:15028015.
- Donnelly, M.J. 2001. 98–536: U.S. Merchandise Trade statistics: 1948–2000. CRS Report for Congress. Available from [www.cnie.org/nle/crsreports/economics/econ-54.cfm](http://www.cnie.org/nle/crsreports/economics/econ-54.cfm) [accessed March 2009].
- Drake, J.A., Mooney, H.A., Di Castri, F., Groves, R.H., Krueger, F.J., Rejmanke, M., and Williamson, M. 1989. *Biological invasions: A global perspective.* John Wiley and Sons, Chichester, UK.
- Durrett, R., and Levin, S.A. 1994. The importance of being discrete (and spatial). *Theor. Popul. Biol.* **46**(3): 363–394. doi:10.1006/tpbi.1994.1032.
- Eiswerth, M.E., and van Kooten, G.C. 2002. The economics of invasive species management: Uncertainty, economics, and the spread of an invasive plant species. *Am. J. Agric. Econ.* **84**(5): 1317–1322. doi:10.1111/1467-8276.00396.
- Elith, J., Burgman, M.A., and Regan, H.M. 2002. Mapping epistemic uncertainties and vague concepts in predictions of species distribution. *Ecol. Model.* **157**(2-3): 313–329. doi:10.1016/S0304-3800(02)00202-8.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., and Zimmermann, N.E. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**: 129–151. doi:10.1111/j.2006.0906-7590.04596.x.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., and Webster, J.R. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* **3**(9): 479–486. doi:10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2.
- Fagan, M.E., and Peart, D.R. 2004. Impact of the invasive shrub glossy buckthorn (*Rhamnus frangula* L.) on juvenile recruitment by canopy trees. *For. Ecol. Manage.* **194**(1-3): 95–107. doi:10.1016/j.foreco.2004.02.015.
- FAO-IPPC. 2006. Guidelines for regulating wood packaging material in international trade. ISPM No.15 (2002). *In International standards for phytosanitary measures. Edited by FAO-IPPC.* Rome, Italy. pp. 174–183.
- FHTET. 2007. Sirex woodwasp risk maps. US Department of Agriculture, Forest Health Technology Enterprise Team. Available from [www.fs.fed.us/foresthealth/technology/invasives\\_sirexnoctilio\\_riskmaps.shtml](http://www.fs.fed.us/foresthealth/technology/invasives_sirexnoctilio_riskmaps.shtml) [accessed March 2009].
- Finnoff, D., Shogren, J.F., Leung, B., and Lodge, D. 2005. The importance of bioeconomic feedback in invasive species management. *Ecol. Econ.* **52**: 367–381.
- Fox, G., Beke, J., Hopkin, T., and McKenney, D. 1997. A framework for the use of economic thresholds in forest pest management. *For. Chron.* **73**: 331–339.
- Frappier, B., and Eckert, R.T. 2003. Utilizing the USDA PLANTS database to predict exotic woody plant invasiveness in New Hampshire. *For. Ecol. Manage.* **185**(1-2): 207–215. doi:10.1016/S0378-1127(03)00256-1.
- Fraser, R.W., Cook, D.C., Mumford, J.D., Wilby, A., and Waage, J.K. 2006. Managing outbreaks of invasive species: eradication versus suppression. *Int. J. Pest Manage.* **52**(4): 261–268. doi:10.1080/09670870600795930.
- Gevrey, M., and Worner, S.P. 2006. Prediction of global distribution of insect pest species in relation to climate by using an ecological informatics method. *J. Econ. Entomol.* **99**(3): 979–986. PMID:16813340.
- Gevrey, M., Worner, S., Kasabov, N., Pitt, J., and Giraudel, J.L. 2006. Estimating risk of events using SOM models: a case study on invasive species establishment. *Ecol. Model.* **197**(3-4): 361–372. doi:10.1016/j.ecolmodel.2006.03.032.
- Gillis, M.D. 2001. Canada's National Forest Inventory (responding to current information needs). *Environ. Monit. Assess.* **67**(1/2): 121–129. doi:10.1023/A:1006405820244. PMID:11339694.
- Giraudel, J.-L., Aurelle, D., and Lek, S. 2000. Application of the self-organizing mapping and fuzzy clustering microsatellite data: How to detect genetic structure in brown trout (*Salmo trutta*) populations. *In Artificial neuronal networks: application*

- to ecology and evolution. *Edited by S. Lek and J.F. Guegan*. Springer-Verlag, Heidelberg, Germany. pp. 187–201.
- Haack, R.A. 2006. Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. *Can. J. For. Res.* **36**(2): 269–288. doi:10.1139/x05-249.
- Hastings, A. 1996. Models of spatial spread: Is the theory complete? *Ecology*, **77**(6): 1675–1679. doi:10.2307/2265772.
- Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmen-dorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C., and Thompson, D. 2005. The spatial spread of invasions: New developments in theory and evidence. *Ecol. Lett.* **8**(1): 91–101. doi:10.1111/j.1461-0248.2004.00687.x.
- Haugen, D.A., and Hoebeke, E.R. 2005. Pest alert *Sirex* wood-wasp – *Sirex noctilio* F. (Hymenoptera: Siricidae). NA-PR-07-05. USDA Forest Service.
- Henderson-Sellers, B., and Henderson-Sellers, A. 1996. Sensitivity evaluation of environmental models using fractional factorial experimentation. *Ecol. Model.* **86**(2-3): 291–295. doi:10.1016/0304-3800(95)00066-6.
- Herborg, L.-M., Jerde, C.L., Lodge, D.M., Ruiz, G.M., and MacI-saac, H.J. 2007. Predicting invasion risk using measures of introduction effort and environmental niche models. *Ecol. Appl.* **17**(3): 663–674. doi:10.1890/06-0239. PMID:17494387.
- Higgins, S.I., and Richardson, D.M. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. *Am. Nat.* **153**(5): 464–475. doi:10.1086/303193.
- Higgins, S.I., Azorin, E.J., Cowling, R.M., and Morris, M.J. 1997. A dynamic ecological-economic model as a tool for conflict resolution in an invasive alien-plant, biological control and native-plant scenario. *Ecol. Econ.* **22**(2): 141–154. doi:10.1016/S0921-8009(97)00574-0.
- Higgins, S.I., Richardson, D.M., Cowling, R.M., and Trinder-Smith, T.H. 1999. Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. *Conserv. Biol.* **13**(2): 303–313. doi:10.1046/j.1523-1739.1999.013002303.x.
- Higgins, S.I., Richardson, D.M., and Cowling, R.M. 2001. Validation of a spatial simulation model of a spreading alien plant population. *J. Appl. Ecol.* **38**(3): 571–584. doi:10.1046/j.1365-2664.2001.00616.x.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**(15): 1965–1978. doi:10.1002/joc.1276.
- Hill, G., and Greathead, D. 2000. Economic evaluation in classical biological control. *In* The economics of biological invasions. *Edited by C. Perrings, M. Williamson, and S. Dalmazzone*. Edward Elgar, Cheltenham, UK. pp. 208–223.
- Holmes, E.E. 1993. Are diffusion models too simple — a comparison with telegraph models of invasion. *Am. Nat.* **142**(5): 779–795. doi:10.1086/285572.
- Horan, R.D., Perrings, C., Lupi, F., and Bulte, E.H. 2002. Biological pollution prevention strategies under ignorance: The case of invasive species. *Am. J. Agric. Econ.* **84**(5): 1303–1310. doi:10.1111/1467-8276.00394.
- Hovestadt, T., Messner, S., and Poethke, H.J. 2001. Evolution of reduced dispersal mortality and ‘fat-tailed’ dispersal kernels in autocorrelated landscapes. *Proc. R. Soc. Lond. B. Biol. Sci.* **268**: 385–391. doi:10.1098/rspb.2000.1379.
- Jarvis, C.H., and Baker, R.H.A. 2001. Risk assessment for non-indigenous pests: I. mapping the outputs of phenology models to assess the likelihood of establishment. *Divers. Distrib.* **7**(5): 223–235. doi:10.1046/j.1366-9516.2001.00113.x.
- Jules, E.S., Kauffman, M.J., Ritts, W.D., and Carroll, A.L. 2002. Spread of an invasive pathogen over a variable landscape: A nonnative root rot on Port Orford cedar. *Ecology*, **83**: 3167–3181.
- Juliá, R., Holland, D.W., and Guenther, J. 2007. Assessing the economic impact of invasive species: the case of yellow starthistle (*Centaurea solstitialis* L.) in the rangelands of Idaho, USA. *J. Environ. Manage.* **85**(4): 876–882. doi:10.1016/j.jenvman.2006.10.024. PMID:17257736.
- Keeney, R.L., and Raiffa, H. 1976. *Decisions with Multiple Objectives*. Wiley, New York, NY.
- Keller, R.P., Lodge, D.M., and Finnoff, D.C. 2007. Risk assessment for invasive species produces net bioeconomic benefits. *Proc. Natl. Acad. Sci. U.S.A.* **104**(1): 203–207. doi:10.1073/pnas.0605787104. PMID:17190819.
- Kelly, M., Guo, Q., Liu, D., and Shaari, D. 2007. Modeling the risk for a new invasive forest disease in the United States: an evaluation of five environmental niche models. *Comput. Environ. Urban*, **31**(6): 689–710. doi:10.1016/j.compenvurbysys.2006.10.002.
- Khalanski, M. 1997. Industrial and ecological consequences of the introduction of new species in continental aquatic ecosystems: the zebra mussel and other invasive species. *B. Fr. Pêche. Piscic.* **344**(5): 385–404.
- Kinezaki, N., Kawasaki, K., Takasu, F., and Shigesada, N. 2003. Modeling biological invasions into periodically fragmented environments. *Theor. Popul. Biol.* **64**(3): 291–302. doi:10.1016/S0040-5809(03)00091-1. PMID:14522170.
- Kolar, C.S., and Lodge, D.M. 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* **16**(4): 199–204. doi:10.1016/S0169-5347(01)02101-2. PMID:11245943.
- Kot, M., Lewis, M.A., and Van den Driessche, P. 1996. Dispersal data and the spread of invading organisms. *Ecology*, **77**(7): 2027–2042. doi:10.2307/2265698.
- Latimer, A.M., Silander, J.A., Jr., Gelfand, A.E., Rebelo, A.G., and Richardson, D.M. 2004. Quantifying threats to biodiversity from invasive alien plants and other factors: A case study from the Cape Floristic Region. *S. Afr. J. Sci.* **100**: 81–86.
- Leeuwen, G.C.M., Baayen, R.P., and Jeger, M.J. 2001. Pest risk assessment for the countries of the European Union (as PRA area) on *Monilinia fructicola*. *EPP0 Bulletin*, **31**(4): 481–487. doi:10.1111/j.1365-2338.2001.tb01030.x.
- Lek, S., and Guegan, J.F. 1999. Artificial neural networks as a tool in ecological modelling, an introduction. *Ecol. Model.* **120**(2-3): 65–73. doi:10.1016/S0304-3800(99)00092-7.
- Lek, S., Delacoste, M., Baran, P., Dimopoulos, I., Lauga, J., and Aulagnier, S. 1996. Application of neural networks to modelling nonlinear relationships in ecology. *Ecol. Model.* **90**(1): 39–52. doi:10.1016/0304-3800(95)00142-5.
- LeSage, J.P., and Kelley Pace, R. 2005. *Spatial Econometric Modeling of Origin-Destination Flows*. Working paper. Available from www.spatial-econometrics.com [accessed March 2009].
- LeSage, J.P., and Polasek, W. 2006. Incorporating transportation network structure in spatial econometric models of commodity flows. *Economics Series 188*. Institute for Advanced Studies.
- Leung, B., Lodge, D.M., Finnoff, D., Shogren, J.F., Lewis, M.A., and Lambert, G. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proc Biol Sci*, **269**(1508): 2407–2413. doi:10.1098/rspb.2002.2179. PMID:12495482.
- Leung, B., Finnoff, D., Shogren, J.F., and Lodge, D. 2005. Managing invasive species: rules of thumb for rapid assessment. *Ecol. Econ.* **55**(1): 24–36. doi:10.1016/j.ecolecon.2005.04.017.
- L Levine, J.M., and D’Antonio, C.M. 2003. Forecasting biological invasions with increasing international trade. *Conserv. Biol.* **17**(1): 322–326. doi:10.1046/j.1523-1739.2003.02038.x.

- Liebholt, A.M., and Tobin, P.C. 2008. Population ecology of insect invasions and their management. *Ann. Rev. Ent.* **53**(1): 387–408. doi:10.1146/annurev.ento.52.110405.091401.
- Lippitt, C.D., Rogan, J., Toledano, J., Sangermano, F., Eastman, J.R., Mastro, V., and Sawyer, A. 2008. Incorporating anthropogenic variables into a species distribution model to map gypsy moth risk. *Ecol. Model.* **210**(3): 339–350. doi:10.1016/j.ecolmodel.2007.08.005.
- Little, E.L. 1971. Atlas of United States trees: conifers and important hardwoods. Vol. 1. Miscellaneous Publication 1146. U.S. Department of Agriculture. Available from <http://esp.cr.usgs.gov/data/atlas/little> [accessed March 2009].
- Little, E.L. 1976. Atlas of United States trees: Minor Western hardwoods. Vol. 3. Miscellaneous Publication 1314. U.S. Department of Agriculture. Available from <http://esp.cr.usgs.gov/data/atlas/little> [accessed March 2009].
- Little, E.L. 1977. Atlas of United States trees: Minor Eastern hardwoods. Vol. 4. Miscellaneous Publication 1342. U.S. Department of Agriculture. Available from <http://esp.cr.usgs.gov/data/atlas/little> [accessed March 2009].
- Lowe, T., Cieszewski, C.J., Zasada, M., and Zawadzki, J. 2003. Distributing FIA information onto segmented Landsat Thematic Mapper images stratified with industrial ground data. In Proceedings of the 4th Annual Forest Inventory and Analysis Symposium, 19–21 November 2002, New Orleans, LA. Gen.Tech. Rep. NC-252. Edited by R.E. McRoberts, G.A. Reams, P.C. Van Deusen, W.H. McWilliams, and C.J. Cieszewski. USDA For. Serv., NC Res. Stn., St. Paul, Minn. pp. 111–116.
- Lubina, J., and Levin, S. 1988. The spread of a reinvading species: range expansion in the California sea otter. *Am. Nat.* **131**(4): 526–543. doi:10.1086/284804.
- Lyons, B.D., Jones, G.C., and Wainio-Keizer, K. 2003. The biology and phenology of the emerald ash borer, *Agrilus planipennis*. In Abstracts of Emerald Ash Borer Research and Technology Development Meeting. Report: USDA FHTET-2004-02. Edited by V. Mastro, and R. Reardon. Forest Health Technology Enterprise Team.
- Magarey, R.D., Fowler, G.A., Borchert, D.M., Sutton, T.B., Colunga-Garcia, M., and Simpson, J.A. 2007. NAPPFAST, an internet system for the weather-based mapping of plant pathogens. *Plant Dis.* **91**(4): 336–345. doi:10.1094/PDIS-91-4-0336.
- Marchetti, M.P., Moyle, P.B., and Levine, R. 2004. Alien fishes in California watersheds: Characteristics of successful and failed invaders. *Ecol. Appl.* **14**(2): 587–596. doi:10.1890/02-5301.
- McAusland, C., and Costello, C. 2004. Avoiding invasives: Trade-related policies for controlling unintentional exotic species introductions. *J. Environ. Econ. Manage.* **48**(2): 954–977. doi:10.1016/j.jeem.2003.11.002.
- McCullough, D.G., Work, T.T., Cavey, J.F., Liebhold, A.M., and Marshall, D. 2006. Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. *Biol. Invasions*, **8**(4): 611–630. doi:10.1007/s10530-005-1798-4.
- McKenney, D.W. 2007a. Canada's plant hardiness site- going beyond the zones. Available from [http://planthardiness.gc.ca/ph\\_main.pl?lang=en](http://planthardiness.gc.ca/ph_main.pl?lang=en) [accessed March 2009].
- McKenney, D.W. 2007b. Regional, national and international climate modeling. Available from <http://cfs.nrcan.gc.ca/subsite/glf-c-climate> [accessed March 2009].
- McRoberts, R.E., Holden, G.R., Nelson, M.D., Liknes, G.C., and Gormanson, D.D. 2006. Using satellite imagery as ancillary data for increasing the precision of estimates for the Forest Inventory and Analysis program of the USDA Forest Service. *Can. J. For. Res.* **36**: 2968–2980.
- Meentemeyer, R., Rizzo, D., Mark, W., and Lotz, E. 2004. Mapping the risk of establishment and spread of sudden oak death in California. *For. Ecol. Manage.* **200**(1-3): 195–214. doi:10.1016/j.foreco.2004.06.021.
- Merriam, R.W., and Feil, E. 2002. The potential impact of an introduced shrub on native plant diversity and forest regeneration. *Biol. Invasions*, **4**(4): 369–373. doi:10.1023/A:1023668101805.
- Moffitt, L.J., and Osteen, C.D. 2006. Prioritizing invasive species threats under uncertainty. *Agric. Res. Econ. Rev.* **35**: 41–51.
- Moffitt, L.J., Stranlund, J.K., Field, B.C., and Osteen, C.D. 2006. Robust inspection for invasive species with a limited budget. In New approaches to the economics of plant health. Edited by A.G.J.M. Oude Lansink. Springer, Dordrecht, The Netherlands. pp. 7–22.
- Morales, J.M. 2002. Behavior at habitat boundaries can produce leptokurtic movement distributions. *Am. Nat.* **160**(4): 531–538. doi:10.1086/342076. PMID:18707528.
- Morgan, M.G., and Henrion, M. 1990. Uncertainty: A guide to dealing with uncertainty in quantitative risk and policy analysis. Cambridge University Press, New York.
- Morrison, L.M., Porter, S.D., Daniels, E., and Korzukhin, M.D. 2004. Potential global range expansion of the invasive fire ant, *Solenopsis invicta*. *Biol. Invasions*, **6**(2): 183–191. doi:10.1023/B:BINV.0000022135.96042.90.
- Muirhead, J.R., and MacIsaac, H.J. 2005. Development of inland lakes as hubs in an invasion network. *J. Appl. Ecol.* **42**(1): 80–90. doi:10.1111/j.1365-2664.2004.00988.x.
- Muirhead, J.R., Leung, B., Overdijk, C., Kelly, D.W., Nandakumar, K., Marchant, K.R., and MacIsaac, H.J. 2006. Modelling local and long-distance dispersal of invasive emerald ash borer *Agri-lus planipennis* (Coleoptera) in North America. *Divers. Distrib.* **12**(1): 71–79. doi:10.1111/j.1366-9516.2006.00218.x.
- Nathan, R. 2003. Seeking the secrets of dispersal. *Trends Ecol. Evol.* **18**: 275–276.
- Nathan, R. 2005. Long-distance dispersal research: building a network of yellow brick roads. *Divers. Distrib.* **11**(2): 125–130. doi:10.1111/j.1366-9516.2005.00159.x.
- Neubert, M.G., and Caswell, H. 2000. Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, **81**: 1613–1628.
- Noble, J.V. 1974. Geographic and temporal development of plagues. *Nature*, **250**(5469): 726–729. doi:10.1038/250726a0. PMID:4606583.
- Nyarko, Y., and Olson, L.J. 1991. Stochastic dynamic models with stock-dependent rewards. *J. Econ. Theory*, **55**(1): 161–168. doi:10.1016/0022-0531(91)90063-A.
- Okubo, A., and Levin, S.A. 2002. Diffusion and ecological problems: modern perspectives. Springer, New York.
- Olson, L.J., and Roy, S. 1996. On conservation of renewable resources with stock-dependent random and non-concave production. *J. Econ. Theory*, **70**(1): 133–157. doi:10.1006/jeth.1996.0079.
- Olson, L.J., and Roy, S. 2002. The economics of controlling a stochastic biological invasion. *Am. J. Arg. Econ.* **84**(5): 1311–1316. doi:10.1111/1467-8276.00395.
- O'Sullivan, P., and Ralston, B. 1974. Forecasting intercity commodity transport in the U.S.A. *Reg. Stud.* **8**(2): 191–195. doi:10.1080/09595237400185181.
- Paine, T.D., and Millar, J.G. 2002. Insect pests of eucalypts in California: implications of managing invasive species. *Bull. Entomol. Res.* **92**(02): 147–152. doi:10.1079/BER2002151. PMID:12020373.
- Paruelo, J.M., and Tomasel, F. 1997. Prediction of functional characteristics of ecosystems: a comparison of artificial neural net-

- works and regression models. *Ecol. Model.* **98**(2-3): 173–186. doi:10.1016/S0304-3800(96)01913-8.
- Park, Y.S., Cereghino, R., Compin, A., and Lek, S. 2003. Applications of artificial neural networks for patterning and predicting aquatic insect species richness in running waters. *Ecol. Model.* **160**(3): 265–280. doi:10.1016/S0304-3800(02)00258-2.
- Pearson, R.G., and Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **12**(5): 361–371. doi:10.1046/j.1466-822X.2003.00042.x.
- Perrings, C., Williamson, M., and Dalmazzone, S. (Editors). 2000. *The Economics of biological invasions*. Edward Elgar, Cheltenham, UK.
- Perrings, C., Dehnen-Schmutz, K., Touza, J., and Williamson, M. 2005. How to manage biological invasions under globalization. *Trends Ecol. Evol.* **20**(5): 212–215. doi:10.1016/j.tree.2005.02.011. PMID:16701371.
- Peter, B., and Nelson, J. 2005. Estimating harvest schedules and profitability under the risk of fire disturbance. *Can. J. For. Res.* **35**(6): 1378–1388. doi:10.1139/x05-073.
- Phillips, S.J., Anderson, R.P., and Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* **190**(3-4): 231–259. doi:10.1016/j.ecolmodel.2005.03.026.
- Piel, F., Gilbert, M., De Cannière, C., and Grégoire, J.-C. 2008. Coniferous round wood imports from Russia and Baltic countries to Belgium. A pathway analysis for assessing risks of exotic pest introductions. *Divers. Distrib.* **14**(2): 318–328. doi:10.1111/j.1472-4642.2007.00390.x.
- Pimentel, D., Lach, L., Zuniga, R., and Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience*, **50**(1): 53–64. doi:10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2.
- Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T., and Tsomondo, T. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. *Agric. Ecosyst. Environ.* **84**(1): 1–20. doi:10.1016/S0167-8809(00)00178-X.
- Pimentel, D., Zuniga, R., and Morrison, D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econ.* **52**: 273–288.
- Porojan, A. 2001. Trade flows and spatial effects: The gravity model revisited. *Open Econ. Rev.* **12**(3): 265–280. doi:10.1023/A:1011129422190.
- Rafoss, T. 2003. Spatial stochastic simulation offers potential as a quantitative method for pest risk analysis. *Risk Anal.* **23**(4): 651–661. doi:10.1111/1539-6924.00344. PMID:12926559.
- Raghu, S., Dhileepan, K., and Scanlan, J.C. 2007. Predicting risk and benefit *a priori* in biological control of invasive plant species: a systems modelling approach. *Ecol. Model.* **208**(2-4): 247–262. doi:10.1016/j.ecolmodel.2007.05.022.
- Regan, H.M., Colyvan, M., and Burgman, M.A. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecol. Appl.* **12**(2): 618–628. doi:10.1890/1051-0761(2002)012[0618:ATATOU]2.0.CO;2.
- Reichard, S.H., and Hamilton, C.W. 1997. Predicting invasions of woody plants introduced into North America. *Conserv. Biol.* **11**(1): 193–203. doi:10.1046/j.1523-1739.1997.95473.x.
- Ricciardi, A. 2003. Predicting the impacts of an introduced species from its invasion history: An empirical approach applied to zebra mussel invasions. *Freshw. Biol.* **48**(6): 972–981. doi:10.1046/j.1365-2427.2003.01071.x.
- Rinella, M.J., and Luschei, E.C. 2007. Hierarchical Bayesian methods estimate invasive weed impacts at pertinent spatial scales. *Biol. Invasions*, **9**(5): 545–558. doi:10.1007/s10530-006-9057-x.
- Rouget, M., and Richardson, D.M. 2003. Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. *Am. Nat.* **162**(6): 713–724. doi:10.1086/379204. PMID:14737709.
- Royama, T. 1992. *Analytical population dynamics*. Chapman & Hall, London, UK.
- Russell, E.W.B. 1987. Pre-blight distribution of *Castanea dentata* (Marsh.). *Borkh. B. Torrey Bot. Club*, **114**(2): 183–190. doi:10.2307/2996129.
- Saphores, J.M., and Shogren, J.F. 2005. Managing exotic pests under uncertainty: Optimal control actions and bioeconomic investigations. *Ecol. Econ.* **52**: 327–339.
- Sharov, A.A., and Colbert, J.J. 1996. A model for testing hypotheses of gypsy moth *Lymantria dispar* L., population dynamics. *Ecol. Model.* **84**(1-3): 31–51. doi:10.1016/0304-3800(94)00110-3.
- Sharov, A.A., and Liebhold, A.M. 1998. Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. *Ecol. Appl.* **8**(4): 1170–1179. doi:10.1890/1051-0761(1998)008[1170:MOSTSO]2.0.CO;2.
- Sharov, A.A., Liebhold, A.M., and Roberts, E.A. 1998. Optimizing the use of barrier zones to slow the spread of gypsy moth (Lepidoptera: Lymantriidae) in North America. *J. Econ. Ent.* **91**: 165–174.
- Shigesada, N., and Kawasaki, K. 1997. *Biological invasions: theory and practice*. Oxford University Press, Oxford.
- Shigesada, N., Kawasaki, K., and Takeda, Y. 1995. Modeling stratified diffusion in biological invasions. *Am. Nat.* **146**(2): 229–251. doi:10.1086/285796.
- Shogren, J. 2000. Risk reduction strategies against the 'explosive invader'. In *The Economics of Biological Invasions*. Edited by C. Perrings, S. Dalmazzone, and M. Williamson. Edward Elgar, Cheltenham, UK. pp. 56–69.
- Skalski, G.T., and Gilliam, J.F. 2003. A diffusion-based theory of organism dispersal in heterogeneous populations. *Am. Nat.* **161**(3): 441–458. doi:10.1086/367592. PMID:12699223.
- Smith, M.T., Bancroft, J., and Tropp, J. 2002. Age-specific fecundity of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on three tree species infested in the United States. *Environ. Entomol.* **31**: 76–83.
- Solla, A., Martín, J.A., Ouellette, G.B., and Gil, L. 2005. Influence of plant age on symptom development in *Ulmus minor* following inoculation by *Ophiostoma novo-ulmi*. *Plant Dis.* **89**(10): 1035–1040. doi:10.1094/PD-89-1035.
- StatsCan. 2003a. Shipping in Canada 2000. Catalogue no. 54-205-XIE. Statistics Canada. Available from [www.statcan.ca/english/freepub/54-205-XIE/0000054-205-XIE.pdf](http://www.statcan.ca/english/freepub/54-205-XIE/0000054-205-XIE.pdf) [accessed March 2009].
- StatsCan. 2003b. Shipping in Canada 2001. Catalogue no. 54-205-XIE. Statistics Canada. Available from [www.statcan.ca/english/freepub/54-205-XIE/0000154-205-XIE.pdf](http://www.statcan.ca/english/freepub/54-205-XIE/0000154-205-XIE.pdf) [accessed March 2009].
- StatsCan. 2004. Shipping in Canada 2002. Catalogue no. 54-205-XIE. Statistics Canada. Available from [www.statcan.ca/english/freepub/54-205-XIE/0000254-205-XIE.pdf](http://www.statcan.ca/english/freepub/54-205-XIE/0000254-205-XIE.pdf) [accessed March 2009].
- StatsCan. 2005. Shipping in Canada 2003. Catalogue no. 54-205-XIE. Statistics Canada. Available from [www.statcan.ca/english/freepub/54-205-XIE/0000354-205-XIE.pdf](http://www.statcan.ca/english/freepub/54-205-XIE/0000354-205-XIE.pdf) [accessed March 2009].
- StatsCan. 2007. Shipping in Canada 2004. Catalogue no. 54-205-XIE. Statistics Canada. Available from [www.statcan.ca/english/freepub/54-205-XIE/54-205-XIE2004000.pdf](http://www.statcan.ca/english/freepub/54-205-XIE/54-205-XIE2004000.pdf) [accessed March 2009].

- StatsCan. 2008a. Merchandise imports and exports, by major groups and principal trading areas for all countries (annual 1971 to 2007) [D397916]. Table 228–0003: Requested from CANSIM database. Statistics Canada. Available from <http://cansim2.statcan.ca> [accessed March 2009].
- StatsCan. 2008b. Imports, exports and trade balance of goods on a balance-of-payments basis, by country or country grouping. Statistics Canada. Available from [www40.statcan.ca/101/cst01/gble-c02a.htm](http://www40.statcan.ca/101/cst01/gble-c02a.htm) [accessed March 2009].
- Stephenson, N.L. 1990. Climate control of vegetation distribution: the role of the water balance. *Am. Nat.* **135**(5): 649–670. doi:10.1086/285067.
- Stewart, T.J. 1992. A critical survey on the status of multiple criteria decision making theory and practice. *Omega*, **20**(5-6): 569–586. doi:10.1016/0305-0483(92)90003-P.
- Swartzman, G.L., and Kaluzny, S.P. 1987. Ecological simulation primer. MacMillan Publ. Co., New York, NY.
- Sydnor, T.D., Bumgardner, M., and Todd, A. 2007. The potential economic impacts of emerald ash borer (*Agrilus planipennis*) on Ohio, U.S., communities. *Arboriculture and Urban Forestry*, **33**: 48–54.
- Thuiller, W., Richardson, D.M., Pysek, P., Midgley, G.F., Hughes, G.O., and Rouget, M. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Glob. Change Biol.* **11**(12): 2234–2250. doi:10.1111/j.1365-2486.2005.001018.x.
- Turchin, P., and Thoeny, W.T. 1993. Quantifying dispersal of southern pine beetles with mark-recapture experiments and a diffusion model. *Ecol. Appl.* **3**(1): 187–198. doi:10.2307/1941801.
- UNCTAD. 2007 Review of Maritime Transport. United Nations Conference on Trade and Development, Geneva, Switzerland.
- US OTA. 1993. Harmful Non-Indigenous Species in the United States. United States Congress, U.S. Congress, Office of Technology Assessment, Wash.
- USACE. 2006. U.S. waterway data: Foreign cargo inbound and outbound. US Army Corps of Engineers. Available from [www.iwr.usace.army.mil/ndc/db/foreign/data](http://www.iwr.usace.army.mil/ndc/db/foreign/data) [accessed March 2009].
- USDA Forest Service. 2007. Forest inventory and analysis database: Database description and users guide version 3.0. U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis Program. Available from [www.fia.fs.fed.us/tools-data/docs/pdfs/FIADB\\_user%20guide%203-0\\_P3\\_6\\_01\\_07.pdf](http://www.fia.fs.fed.us/tools-data/docs/pdfs/FIADB_user%20guide%203-0_P3_6_01_07.pdf) [accessed March 2009].
- van den Bosch, F., Hengeveld, R., and Metz, J.A.J. 1992. Analysing the velocity of animal range expansion. *J. Biogeogr.* **19**(2): 135–150. doi:10.2307/2845500.
- von Winterfeldt, D., and Edwards, W. 1986. Decision analysis and behavioral research. Carbridge University Press, London.
- Veltman, C.J., Nee, S., and Crawley, M.J. 1996. Correlates of introduction success in exotic New Zealand birds. *Am. Nat.* **147**(4): 542–557. doi:10.1086/285865.
- Waage, J.K., Fraser, R.W., Mumford, J.D., Cook, D.C., and Wilby, A. 2005. A new agenda for biosecurity. A Report for the Department for Food, Environment and Rural Affairs. Faculty of Life Sciences, Imperial College London, London, UK.
- Wald, A. 1945. Statistical decision functions which minimize the maximum risk. *Ann. Math.* **46**(2): 265–280. doi:10.2307/1969022.
- Walley, P. 1991. Statistical reasoning with imprecise probabilities. Chapman and Hall, London, UK.
- Watkinson, A.R., Freckleton, R.P., and Dowling, P.M. 2000. Weed invasions of Australian farming systems: From ecology to economics. *In* The economics of biological invasions. Edited by C. Perrings, M. Williamson, and S. Dalmazzone. Edward Elgar, Cheltenham, UK. pp. 94–114.
- Watts, M.J., and Worner, S.P. 2004. Comparison of a self organising map and simple evolving connectionist system for predicting insect pest establishment. *Int. J. Information Technol.* **12**(6): 35–42.
- Weinberger, H.F. 2002. On spreading speeds and traveling waves for growth and migration models in a periodic habitat. *J. Math. Biol.* **45**(6): 511–548. doi:10.1007/s00285-002-0169-3. PMID: 12439589.
- Weintraub, A., and Navon, D. 1976. A forest management planning model integrating silvicultural and transportation activities. *Manage. Sci.* **22**(12): 1299–1309. doi:10.1287/mnsc.22.12.1299.
- Westphal, M.I., Browne, M., MacKinnon, K., and Noble, I. 2008. The link between international trade and the global distribution of invasive alien species. *Biol. Invasions*, **10**(4): 391–398. doi:10.1007/s10530-007-9138-5.
- Williamson, M. 1996. Biological invasions. Chapman and Hall, London.
- Wittwer, G., McKirdy, S., and Wilson, R. 2005. Regional economic impacts of a plant disease incursion using a general equilibrium approach. *Aust. J. Agric. Resour. Econ.* **49**(1): 75–89. doi:10.1111/j.1467-8489.2005.00276.x.
- Woodbury, P.B. 2003. Dos and don'ts of spatially explicit ecological risk assessments. *Environ. Toxicol. Chem.* **22**(5): 977–982. doi:10.1897/1551-5028(2003)022<0977:DADOSE>2.0.CO;2. PMID:12729206.
- Worner, S.P., and Gevrey, M. 2006. Modelling global insect pest species assemblages to determine risk of invasion. *J. Appl. Ecol.* **43**(5): 858–867. doi:10.1111/j.1365-2664.2006.01202.x.
- WTO. 1993. Agreement on the application of sanitary and phytosanitary measures. World Trade Organization, Geneva.
- Yachi, S., Kawasaki, K., Shigesada, N., and Teramoto, E. 1989. Spatial patterns of propagating waves of fox rabies. *Forma*, **4**: 3–12.
- Yamamura, K., Katsumata, H., and Watanabe, T. 2001. Estimating invasion probabilities: A case study of fire blight disease and the importation of apple fruits. *Biol. Invasions*, **3**(4): 373–378. doi:10.1023/A:1015850422395.
- Yemshanov, D., McKenney, D.W., de Groot, P., Haugen, D., Siders, D., and Joss, B. 2009a. A bioeconomic approach to assess the impact of an alien invasive insect on timber supply and harvesting: A case study with *Sirex noctilio* in eastern Canada. *Can. J. For. Res.* **39**(1): 154–168. doi:10.1139/X08-164.
- Yemshanov, D., Koch, F.H., McKenney, D.W., Downing, M.C., and Sapio, F. 2009b. Mapping invasive species risks with stochastic models: a cross-border US-Canada application for *Sirex noctilio* Fabricius. *Risk Anal.* **29**(6): 868–884. doi:10.1111/j.1539-6924.2009.01203.x. PMID:19220798.
- Zalba, S.M., Sonaglioni, M.I., Compagnoni, C.A., and Belenguer, C.J. 2000. Using a habitat model to assess the risk of invasion by an exotic plant. *Biol. Conserv.* **93**(2): 203–208. doi:10.1016/S0006-3207(99)00146-9.