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Overview on modelling tools used in management strategies for invasive insect species

Abstract - To deal with the increased frequency and magnitude of invasive species, risk-based strategies for decision-support are designed. In several strategic areas, modelling tools are indispensable and used among others, for the identification of risks (maps of potential distributions) and the analysis of treatment options (containment of already established species). This chapter provides a brief overview on modelling tools designed for describing the potential distributions of invasive species (statistical descriptions, mechanistic models) and their spread. With respect to the spread, modelling tools are developed on the basis of the mean-field assumption (statistical models, phenomenological models) and models that are not constraint by this assumption (continuous dynamic models, individual-based models, grid-based (lattice) models, metapopulation models).

In the area of risk identification and potential distributions of invasive species, three tools are used. The first tool exclusively takes into account the climatic requirements of the invasive species, the second tool focuses on the population ecology and management, and the third tool treats them as members of communities and applies methods of community ecology to their study and management.

In the area of the analysis of risk treatment options and the design of containment strategies, ecologists and entomologists also rely on a wide range of different methodologies. Some tools appear to be suitable for homogeneous environments and large-scale dispersal processes. Other models are appropriate for low density populations and high biological and environmental variability. There are also modelling tools that take into account spatial heterogeneity and fragmented landscapes. The selection of modelling tools depends on the quality of the ecological system under study and management as well as on the objectives to be met. In general, modelling tools are not seen as an end-product of a project but continuously changed in response to new information and needs.

Riassunto - *Rassegna dei modelli utilizzati nelle strategie di gestione delle specie di insetti invasive*

Nella gestione delle problematiche connesse alla frequenza e alla importanza delle specie invasive svolgono un ruolo importante strategie a supporto delle

decisioni basate sull'analisi del rischio. Nell'ambito di tali strategie i modelli svolgono un ruolo fondamentale, per esempio nella identificazione del rischio (mappe per la distribuzione potenziale) e nella analisi delle opzioni di trattamento (per il contenimento di specie già stabilitesi in un dato territorio). Questo lavoro ha lo scopo di fornire una breve rassegna sui modelli sviluppati per descrivere la distribuzione potenziale delle specie (modelli statistici e modelli meccanicistici) e la loro diffusione. Relativamente al problema della diffusione sono stati sviluppati e impiegati modelli che sono basati sulla assunzione del campo-medio (modelli statistici e modelli fenomenologici) e modelli che non richiedono tale assunzione (modelli dinamici in spazio continuo, modelli individual-based, modelli a griglia, modelli di metapopolazione).
Nell'ambito della definizione del rischio e della distribuzione potenziale delle specie invasive sono principalmente utilizzati tre tipi di strumenti. Il primo è basato esclusivamente sulla considerazione delle necessità climatiche delle specie invasive, il secondo è basato su modelli utilizzati nella ecologia e nella gestione delle popolazione e il terzo considera le specie invasive come membri di biocenosi e applica per il loro studio e la loro gestione i metodi della ecologia di comunità.
Anche nell'ambito dell'analisi del rischio associato a differenti opzioni di trattamento e a diverse strategie di contenimento, gli ecologi e gli entomologi fanno riferimento ad una ampia gamma di metodologie. Alcuni modelli sono adatti per ambienti omogenei e processi di dispersione a larga scala. Altri sono appropriati per popolazioni a bassa densità e ambienti caratterizzati da eterogeneità spaziale e frammentazione del paesaggio. La selezione dei modelli dipende inoltre dalle caratteristiche del sistema ecologico oggetto di studio e gestione così come dagli obiettivi da raggiungere. Per concludere, è importante considerare che lo sviluppo di appropriati strumenti di modellistica non deve essere visto come l'obiettivo finale di un progetto; tali strumenti sono infatti oggetto di un cambiamento continuo in funzione della acquisizione di informazioni dal sistema analizzato e delle necssità relative agli interventi.

Key words: invasive species, model, risk identification, potential distribution, spread

INTRODUCTION

The increased connectivity of the global human population has amplified the frequency and effect of biological invasions (Crowl *et al.*, 2008). New trade routes among previously disconnected countries (Aide & Grau, 2004) as well as enhanced transportation technologies have increased both the frequency and magnitude of invasions and potentially deadly diseases worldwide (Crowl *et al.*, 2008). In addition, land-use and climate change interact with human trasportation networks to facilitate the spread of invasive species from local to continental scales (Dukes & Mooney, 1999; Sakai *et al.*, 2001; Crowl *et al.* 2008). Dukes & Mooney (1999) consider biological invasions as important elements of global change. They refer to research suggesting that an increase in nitrogen deposition and CO_2 concentration favour groups of plant and animal species that share traits which allow them to capitalize on the various elements of global change. Hamilton (2008) reported conflicting results of elevated CO_2 on herbivory and interpreted them as as the effect of the arthropod community that overrides the effect on single species.

Invasive species are considered to be one of the major threats to biodiversity and ecosystem function (Kolar & Lodge 2001; Park, 2004; Carrete & Tella, 2008). The introduction of non-native species and range expansions of native species with changing land-use and climate have profound consequences for the ecosystems they occupy (Gómez-Aparicio & Canham, 2008) leading to local and regional extinctions of native species and entire communities, shifts in native species richness and abundance, altered fire regimes, water quality, and biochemical cycles (Crowl *et al.*, 2008), and invasions impose novel selection pressure on native species (Lau, 2008). Invasive species may negatively affect ecosystem service provision, i.e the conditions and processes through which ecosystems sustain and fulfill human life (Daily & Dasgupta, 2001; Tallis & Kareiva, 2006). The estimated environmental and economic costs of non-native species in the US alone is over $ 120 billion annually (Pimentel *et al.*, 2005). Invasive species are also considered as a threat to economic, ecological and social resources (Forrest *et al.*, 2006) and hence, may affect the ecological, economic and social capitals, the sustainability and the resilience of eco-social systems across wide spatial scales (Gilioli & Baumgärtner, 2007; 2008).

For a further discussion of the subject, a clarification of the terms used in invasive species ecology and management appears to be useful. To prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause, Official U.S. definitions regarding invasive species were provided and management aspects were specified in Executive Order 13112 signed by President William Clinton on February 3, 1999 (Anonymous 2008a). Accordingly, "Alien species" means, with respect to a particular ecosystem, any species, including its seeds, eggs, spores, or other biological material capable of propagating that species, that is not native to that ecosystem. "Invasive species" means an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health. As an aside, the literature often refers to "invader" rather than "invasive species" and to "nonindigeneous" rather than "alien" species. Liebhold & Tobin (2008) list arrival, establishment and spread as invasion phases for which management activities are unteraken. They refer to the "arrival" phase in the case of transport of a nonindigeneous species to new areas outside of its native range, to the "establishment" phase if the growth of a population has reached sufficient levels as to make extinction highly unlikely and to the "spread" phase as an expansion of the nonindigeneous species' range into new areas. In the case of "arrival" there are international quarantines and inspections, the "establishment" phase is managed by detection and eradication activities, and the activities for the "spread" phase are domestic quarantines and barrier zones.

To deal with the increasing frequencies and magnitude of introductions, the strategy of managing individual cases of already established invaders on a one by one basis is no longer seen as an efficient management option. Rather, strategies for dealing with the possible and actual introductions of a broad range of organisms across wide spatial scales are required (Forrest *et al.*, 2006; Batabyal, 2007). First, such strategies rely on international and national cooperation. The Convention on Biological Diversity (CBD) and the International Plant Protection Convention (IPPC) oblige contracting parties to undertake actions on invasive alien species at the international level (Anonymous, 2003). The European and Mediterranean Plant Protection Organization (EPPO), responsible for European cooperation in plant protection in the European and Mediterranean region, intends to increase its activities in the area of invasive species. EPPO (2008) will assist members in the prevention of introduction, establishment and spread of invasive alien plants by providing documentation, recommending actions, guidance on measures on eradication and containment. At the regional level, the Centro BioLomb (2005) summarizes the regulations and responsibilities of the European Union, Italy and its regions with respect to alien species. Second, the strategies selected by these actors should include the establishment of networks operating through wide scales (Crowl et al, 2008). The network should a) monitor changes local and geographic distributions of invasive species and infectious diseases, b) predict the processes and environmental conditions that promote the spread of invasive species and disease vectors from individual sites to regions and the continent, and 3) understand the long-term ecological and evolutionary responses to ecosystem invasions. The strategies should also include the design of a risk-based decision-support framework that allows setting prioritities for the management of introductions (Forrest *et al.*, 2006; Batabyal, 2007).

The strategies dealing with the invasions have to take into account the dynamics of complex ecological and social (ecosocial) systems. To deal with ecosystem complexity, Jørgensen (2002), among many others, consider models as indispensable tools for knowledge integration and decision support. For Cannas *et al.* (2003), mathematical models are the most fructiferous approach to understand, predict and control ecological invasions. When developing models, it may be useful to consider the particular ecologies of invasive species exhibiting high rates of population increase and spatial diffusion as well as possibly high ecological and economic impacts. Importantly, model development and use should be seen as a continuous process that takes place in a management context and the comparison of model performance with aspects of their intended use requires continuous adaptations (Hilborn & Mangel, 1997; Petersen, 1996; Rykiel, 1996).

This chapter focus on ecological aspects of the strategy and disregards social management elements that would include the organization of control operations and the adaptation of the society to the challenges resulting from the invasion of alien species strategies. As indicated above, modern societies are at risk of loosing ground not only in ecological but probably also in economic and social dimensions and hence, are advised to face the challenge of invasions in the context of a risk-based decision support system (Forrest *et al.*, 2006). For this context, the chapter provides an overview on modelling tools that appear as particularly important components of management strategies for invasive species. However, a comprehensive review of models dealing with the spatial and temporal dynamics of invaders and their effects on eocosocial systems goes far beyond the scope of this chapter and the reader is referred, for example, to Higgins and Richardson (1996), Dieckmann *et al.* (2000) for additional information. In additions, the chapter focuses on modelling tools, and the reader is referred to Myers *et al.* (2000) and Simberloff (2003) for recent analyses of management options. When selecting examples for illustration purposes, we attempt to highlight some aspects particularly familiar to us. Hence, the choice of the examples is not a reflection of the state of model development.

DECISION-SUPPORT FOR PRIORITY SETTING FOR MANAGING INVASIONS

The work on invasive species requires to take into account different dimensions including management. The heterogeneity of ecological, economic and social components require the design of a management strategy with adequate tools for addressing multifaceted problems. A risk-based decision-support system may provide the context in that some of these tools will be developed and implemented. Of particular interest is the risk-based decision-support framework for marine organisms in New Zealand (Forrest *et al.*, 2006) depicted in Fig. 1. This framework has been developed under the recognition of the threats to environmental, economic, social and cultural resources and the prospects of further incursions and provides a systematic and transparent mechanism for identifying and analyzing risks, and prioritizing management objectives. According to Fig. 1, the framework contains the areas of risk identification, risk assessment, analysis of risk tretament options and risk evaluation. In each area, key elements are given. The discussion of these areas and the methods required goes beyond the scope of the paper, and the reader is referred to Forrest *et al.* (2006) for details.

Models are integral parts of such a strategy because they allow risk analyses on quantitative and objective grounds. Several strategic areas of Fig. 1 rely on the design and use of modelling tools, but only two areas are referred to in this paper (highlighted in italics in Fig. 1). The next section deals with area 1 (Fig. 1) and the predictions on potential spatial distributions of target species and their mapping. The subsequent section 4 deals with third area (Fig 1) and focuses on the containment of established and spreading species. In this case, the species is well established and spreading occurs at different spatial scales with respect to the original colonization areas.

POTENTIAL SPATIAL DISTRIBUTIONS

Potential distributions of invasive species can be predicted on the basis of climatologic data or remotely sensed data with reference to the actual areas of their geographical distributions. As a result, a a potential spatial distribution, often represented on maps, is obtained. In a mechanistic approach, the method is combined with biological information of the species under consideration, and maps are often used to present the predicted areas of potential geographical distributions.

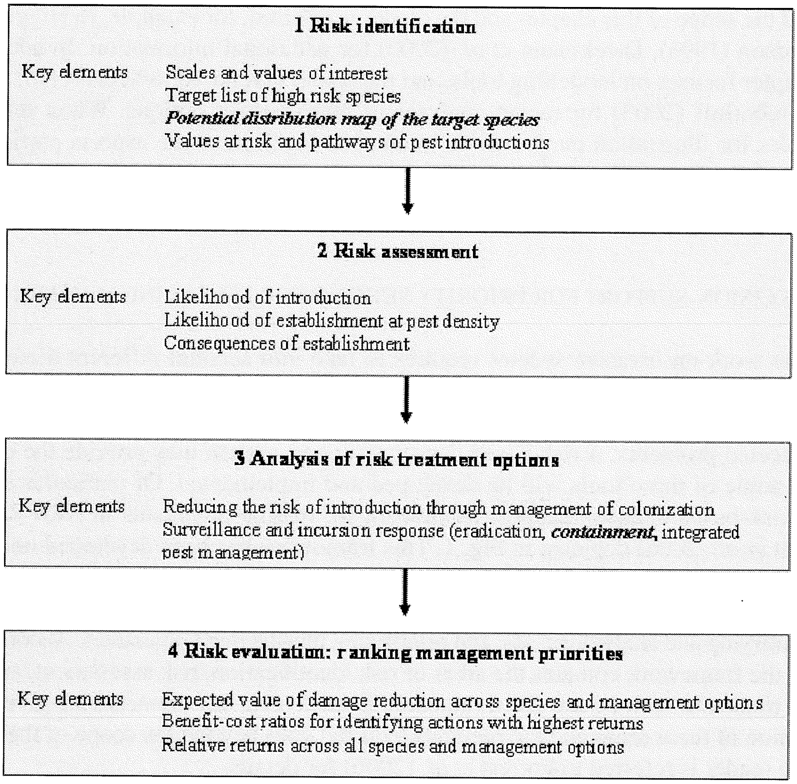

Fig. 1 - Decision-support framework for setting priorities for the management of invasive pests (Forrest *et al.*, 2006, modified). The key element of the different areas in italics require the design and use of the modelling tools that described in this chapter (modified and reproduced with the permission of Springer, Berlin).

Climate matching

CLIMEX (2008) refers to a tool for comparing the climatologic data of different places without reference to any particular species. The CLIMEX simulation and modeling software assist the user in understanding the impact of climate change on species distribution and the potential risk from invasive species to an agricultural region includes a climate-matching function that can be used in the absence of any knowledge of the distribution of a species (Sutherst et al, 2000). The Match Climates option allows the user to directly compare the temperature, rainfall, rainfall pattern and relative humidity of a given location with any number of other locations. It provides a method of identifying sites with similar climates for targeting collection and release sites, or for assessing risks from exotic species.

Statistical analyses

Remote sensing data have been used by Tatem (2005) to outline the potential of large-scale satellite imagery for developing an approach to identify potential future vineyard locations. Rogers (2003) correlated satellite data with disease indicators and produced maps for well documented stuations to obtain robust and reliable correlations. They used the model for early warning purposes and for describing local, regional and continental distributions of vectors and diseases (Rogers *et al.*, 2002; Rogers, 2003). The analyses of remote sensing data could also be useful for precting potential distributions on invasive species.

Mechanistic representation

For single species, the CLIMEX (2008) simulation and modelling software takes into account climatic requirements that are inferred from its known geographical distribution (either in its native range or in another region where it has been established for a long time), relative abundance and seasonal phenology (Sutherst *et al.*, 2000). Some laboratory data, such as developmental threshold temperatures, can be used to fit or fine tune CLIMEX parameter values. Initial estimates of parameter values are fine-tuned by comparing the indices with the known presence or absence, seasonal phenology and, preferably, relative abundance of the species in each location. An Annual Growth Index (GIA) describes the potential for growth of a population during the favourable season. Four Stress Indices (Cold, Hot, Wet and Dry), and in some cases their interactions, describe the extent to which the population is reduced during the unfavourable season. The Growth and Stress Indices are combined into an Ecoclimatic Index (EI), to give an overall measure of favourableness of the location or year for permanent occupation by the target species. Two limiting conditions, ie the length of the growing season and obligate diapause, act as overall constraints to the EI value where relevant. The results are presented as tables, graphs, or maps. Fig. 2 depicts the CLIMEX predication for the distribution of Codling moth (*Cydia pomonell*a) in Australia (Woods & Hardie, 2008).

For single species systems, potential climatic change scenarios have been used as inputs for CLIMEX in an effort to predict the impact of climate change on potential distributions and relative abundances of *Oulema melanopus, Meligethes viridescens* and *Ceutorynchus obstrictus* in Canada (Olfert and Weiss, 2006) where they have recently been introduced. Compared to the predicted range and distribution under current climate conditions, model results indicated that all three species would have increased ranges and relative abundances for temperature increases between 1 and 7 °C. In addition, risks associated with these species will likely become more intense, both in terms of severity in regions where these species presently occur and in terms of their ability to become established in areas they do not occur (Olfert & Weiss, 2006).

For multi-species population systems, models for the temporal dynamics of interacting populations have been developed (Gutierrez, 1996) and could be used for predicting the potential spatial distribution and the development of a species complex including the resource base (plant). The models rely on common functional and numerical response

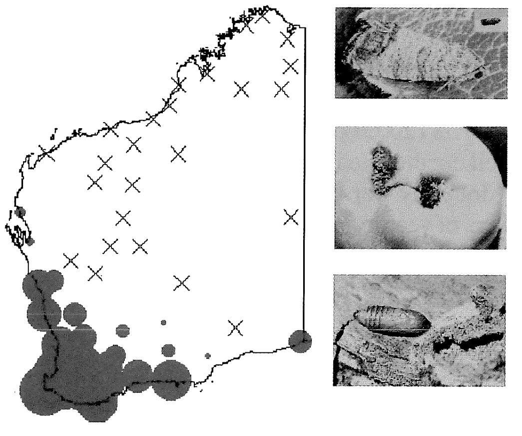

Fig. - CLIMEX prediction for the likely distribution of codling moth (*Cydia pomonella*) in Western Australia in irrigated orchards where it is still absent (Woods & Hardie, 2008). Map reproduced with kind permission of B. Woods and D. Hardie (Senior Entomologists, Department of Agriculture & Food, Western Australia (DAFWA)), Digital images provided courtesy of the Department of Agriculture & Food, Western Australia (DAFWA).

models, and the estimates of parameters are primarily derived from studies carried out under experimental conditions or from model calibrations during the validation process; weather variables and edaphic conditions are the driving variables (Gutierrez & Baumgärtner, 2007). The model output can be integrated in a geographic information system to produce areas of geographical distributions of population system evolution, structure and function at different spatial scales (Gutierrez *et al.*, 2008).

For communities, ecological concepts predict a lower success rate for invading colonists when competition among neighboring species for freely available resources is intense (Lohrer *et al.*, 2008). Although the supply of colonists and the variability of the habitat can override the effects of competition, the negative diversity-invasibility relationships remains theoretically and empirically robust in small-scale highly competitive systems (Tilman, 2004; Zavaleta & Hulvey, 2004). As a corollary to the above, Lohrer *et al.* (2008) expected that, in disturbance-dominated systems, resource limitation is less likely to inhibit colonization, and species richness should have little effect in invasion success. Nevertheless, they found in marine systems decreased invasion with increasing rate of disturbance. These observations can be seen as a components of a conceptual model for dealing with the effects of invasive species at the community ecology level.

MODELLING OF THE SPREAD

The elements of population invasions are viewed in the three phases arrival, establishment and spread (Liebhold & Tobin, 2008). During the first two phases, populations are growing from low densities and expanding into new habitats. Freckleton *et al.* (2006) assume that stochastic factors are important limiting factors. In contrast, following successfull establishment and during the spread phase, populations may be at much higher densities and limiting factors such as density-dependence may dominate population change (Freckleton *et al.*, 2006). Sharov (2008) observes that discontinuous long-distance dispersal usually occurs in combination with short-distance continuous dispersal. The combination of long- and short term dispersal mechanisms is known as stratified dispersal and includes establishment of new colonies, growth of individual colonies and colony coalescence contributing the advance of the population front (Sharov, 2008). Liebhold and Tobin (2008) state that spread is driven by the coupling of population growth with dispersal; while some species spread in spatially continuous manner, most exhibit stratified dispersal which results in discrete jumps that generally increase the rate of spread.

Some models are based on the assumption that the effects of neighbours are proportional to their density averaged across a large spatial domain (mean-field assumption). This assumption is most likely to hold as a good approximation when the physical environment of organism is homogeneous, if physical forces cause strong mixing of organisms, organisms are highly mobile or interact with others over long distances (Law *et al.*, 2000).

In many circumstances, however, the mean-field assumption becomes less and less appropriate. A lack of mixing of individuals generates neighbourhoods around individuals that deviate from spatial averages. Differences in local environment conditions become especially important if organisms only interact over short distances and experience an environment that is different from the environment averaged across the entire ecological habitat (Law *et al.* 2000). If the mean-field assumption cannot be held, the spread may be analysed by continuous or discrete spatial models.

Models with mean field-assumption

Statistical models. Cox *et al.* (2000) developed statistical models for the analysis and interpretation of empirical data and assign them to three main subjects: essentially descriptive statistical models, stochastic models, and more formal statistical methods interrelating models with empirical data. Descriptive statistical models are most useful in the preliminary inspection of data as exemplified by plotting time series data for examination of defective data.

Simple stochastic models are developed for mathematical tractability of the properties and for their important role in providing a framework within which the development of models motivated by specific subject matter can take place. If the value of single function varies over space so that the pattern is generated by its level contours, a suitable model may be built on a Gaussian process. The resulting variogram shows the dependency of the variance on the spatial separation and can be used to interpolate the surface between observed spatial locations, i.e. in kriging procedures. The Colorado Invasive species Mapping Project (Anonymous, 2008b) relies on area-specific species list, environmental and anthropogenic variables from available Geographical Information Systems (GIS) and satellite imageries, and soil maps to create a spatially explicit model of probable non-native species richness using trend surface analysis and kriging, co-kriging or regression tree methods to capture both large and small-scale variability.

However, if the function takes only a discrete set of values, then the pattern will focus on patches that have the same value as exemplified by land use maps or by maps of vegetation types. If the points of interest occur completely at random, model development can be based on a Poisson process. The ratio of the variance to the mean is equal to 1 the data may arise from a Poisson process. For a port survey in the United States, Power *et al.* (2008) relied on Hewitt and Martin (2001) and determined the appropriate sampling effort using the methods of Green and Young (1993) for rare species with a Poisson distribution and concluded that a sample size of approximately 13 samples is necessary to detect a species with a mean Poisson density of 0.1 individuals per sample unit at a 95% probability.

Phenomenological models. The ecological literature contains many experimental studies on movement of usually marked individuals that are released at a specific locations and captured at various distances. The data can either be represented by the frequency distribution of dispersal distances or by the two-dimensional distance functions (Levin *et al.*, 2003). Turchin (1998) presented a general parametric formulation encompassing the commonly used Gaussian, negative binomial and inverse power law functions fitted to dispersal data.

An analysis of variance was carried out and regression models were used to describe the dispersal of released *Cactoblastis cactorum* adults (Hight *et al.*, 2005). The study was part of a sterile insect release program against the invasive *C. cactorum* and consisted of release-recapture experiments to examine the dispersal ability of untreated and treated cactus moth males. The results suggest that an overflooding ratio as low as 5:1 can effectively suppress *C. cactorum* in field cages and that releasing both genders together is more effective than releasing males only. In open field releases, the dispersal ability of *C. cactorum* was not significantly affected by treating the adults with gamma radiation.

A simple logistic regression approach applied to historical records enabled Perrins *et al.* (1993) to examine the rate and extent of the spread of three introduced *Impatiens* spp. plants in the British Isles. Pysek and Prach (1993) fitted an exponential regression model to data on several alien plants in Europe and obtained, via the slope of the regression, an estimate of the invasion rate. In their overview on phenomenological models, Higgins and Richardson (1996) provide also examples for the applications of geometric and Markov models to the spread of alien plants.

The mean-field assumption is also held in populations model that treat diffusion phenomenologically taking into account diffusive operators.

Models without mean-field assumption

Continuous dynamic models. Continuous dynamic models can predict distributions from characteristics of the dispersal process (Levin *et al.*, 2003). The origin of classical diffusion models are fond in Skellam (1951) who modeled the advance of invading species. Dispersal affects the local dynamics of populations and metapopulations, the genetic structure of populations as well the structure and dynamics of communities (Levin & Murrell, 2003). Skellam (1951) described the rate of change of a local population by adding a diffusion component to the classical model on population growth constraint by the carrying capacity. The major problem with this model is the implied normally distributed dispersal of propagules (Levin *et al.*, 2003). There is a tremendous variability in observed data but nevertheless a strong tendency for a large number of distances near the centre and in the tail (Caswell *et al.*, 2003).

The addition of natality and mortality to the classical diffusion models lead to the development of reaction-diffusion models. Marsula and Wissel (1994) used them to simulate a barrier zone that can stop the spread of *Cochliomyia hominivorax*, the New World screw-worm fly. Sharov *et al.* (1998) define a barrier zone as an area at the front of the population distribution where eradication (or suppression) activity is performed in order to prevent or to slow the spread of the population. Marsula and Wissel (1994) estimated the minimum width of the barrier zone and the density of sterile males that is sufficient for stopping the spread.

The reaction-diffusion models can further be developed by introducing a drift component arising from the wind for example. This way, dispersal occurs under the influence of diffusion and advection processes. The reaction-diffusion models with drift have been extended to take into account diffusion into two dimensions (Okubo & Levin, 1989). Wind speed and direction as well as horizontal and vertical speed components have also been built into the dispersal models (Levin *et al.*, 2003).

Invaders may display peak densities moving across a spatial gradient referred to as travelling waves. Johnson *et al.* (2006) did not study invasive species but provide the methodology for studying travelling waves with respect to a tritrophic system in heterogeneous landscapes. To elucidate the demographic mechanism(s) responsible for inducing recurrent outbreak waves across heterogeneous landscapes, they developed a patch-specific model on the dynamics of a tritrophic system (patch quality, Larch bud moth (*Zeiraphera diniana*), parasitoids) and complemented it with a dispersal model for both *Z. diniana* and the parasitoids. A two-dimensional Gaussian model with absorbing boundaries was selected for representing the dispersal, because it is an approximation of redistribution based on a random walk dispersal mode. An analysis of the periodicity in the cycles provides information on the wave epicentre as well as on the direction and speed of travelling waves. The results suggest that recurrent travelling waves originate in high connectivity habitats aggregated around a single focus.

Individual-based models. The essence of the individual-based approach is the derivation of the properties of ecological systems from the properties of the individuals constituting the systems (Łomnicki, 1992): Individual-based models can be motivated by direct observations of individuals in the field, and they force precise thinking about the processes involved (Law et al, 2000). Spatially explicit, individual-based models contrast with spatially implicit models that meet the previously defined mean-field assumption and give striking illustrations of the remarkable behaviour that emerge. Originally, the applicability of individual-based models was particularly recommended for small populations, populations that are subjected to a high degree of time related stochasticity in the environment, and populations in which environmental exposure and encounters with other individuals are likely to vary greatly in space (DeAngelis & Rose, 1992; Di Cola *et al.*, 1999). Thus, individual-based models may be appropriate modelling tools at the beginning of an invasion and for dealing with invaders entering a spatially heterogenous habitat at low densities

An individual-based model has been used, for example, to assess the invasion status of the plant *H. mantegazzianum* (Nehrbass & Winkler, 2007). The results illustrate that, in contrast to the predictions of a transition matrix model, the invasion status of *H. mantegazzianum* has not changed and that populations are still expanding in space. This is due to the individual variability which is accounted for in the individual-based model but missing in the matrix model. The studies also show that, although the long-term average of the population growth rate is large and populations generally expand, there are years in which populations decline.

Grid-based (lattice) models. The spread of a single invasive plant species is studied by Oppenheimer and Ervin (2007). The geographic spread of a wind-dispersed invasive shrub, as influenced by human disturbances that provide open-canopied low competition habitat. They developed a preliminary hybrid lattice model operating in two stages. The model divides the domain into spatial nodes, each of which has a carrying capacity and intrinsic growth rate for a continuous logistic growth model for plant population. There is then a seed dispersal stage with each lattice node having a probability of plant establishment depending on seed load. The old population is taken as the initial condition in previously occupied nodes and the established seedling population is taken as the initial condition in formally unoccupied node and the logistic stage is run again. Siegert *et al.* (2006) studied the emerald ash borer (EAB), *Agrilus planipennis*, a destructive tree pest and responsible for the death and decline of over 15 million ash trees in southeastern lower Michigan since its establishment in North America. Tree ring analyses are performed on trees preferentially collected over declining or non-stressed ash trees on at least a 3.0 × 3.0 mile sampling grid over an area greater than 5800 square miles encompassing the core EAB infestation. Crossdating and other dendrochronological analyses are in progress that will reveal when and where EAB initially became established in southeastern lower Michigan and how it spread historically. Additional ongoing research includes developing dynamic coupled map lattice models of EAB spread and dispersal parameterized to match EAB dynamics observed at several outlier sites.

For studying the invasion process, the Cellular Automata (CA) are considered as especially useful (Cannas *et al.*, 2003). Cole and Albrecht (2008) provide a description of CA's that, formally, are composed of the four elements *cell*, *state*, *neighborhood* and *rule*. A CA consists of a regular uniform lattice, which could be infinite in extent. The square *cells* of the lattice make up the cellular space The state of a cell depends on the states of other cells in the neighbourhood of that specific cell. The *neighborhood* is defined by the immediately adjacent cells. The state or value of the cell is updated according to the neighbouring pixel. The updating of pixels takes place in discrete time steps according to fixed *rules*. Cole and Albrecht (2008) employ CA's coded within a Geographic Information System (GIS) to test the ability of studied parameters of vegetation dynamics to represent spatial growth patterns. Their method combines the well-established spatial data management and presentation capabilities of GIS with the spatial and temporal modeling capabilities of CA theory, creating the ideal tool for applied, data rich modeling. Moreover, instead of conventionally testing a previously created model, parameters are examined through simulation for their contribution to spread and the resulting spatial pattern.CA's have been applied to the spread of single and interacting species. Cannas et al (2003) developed a one species CA and proceede therafter to interacting mutiple CA. The first model takes into account life history traits of the species relevant to population dynamics and the colonization probability. The second model takes also into account competition and applies three rules. Here, we only refer to rule 1 according to that a given cell cannot be occupied by individuals of different species at the same time. The results of the simulation study showed the mean seed dispersal distance and minimum reproductive age were the main factors influencing invasion velocity.

Additional elements have been considered by Parks *et al.* (2005) who developed a stochastic species spread model using an agent-based modelling approach with CA to account for spatial relationships and changes in those relationships over time. The agent-based approach assigns numerous properties, including the percent of the grid point infested, to each of the 1240 grid points with 6 km distances

Metapopulation models. Metapopulations are systems of local populations connected by dispersing individuals. Metapopulation models have been applied to the plants *Nasella trichotoma* and *Avena fatua* invading Australia (Higgins & Richardson, 1996). The landscape has been divided into discrete local population sites, each of which supports exponential population growth. A proportion of each local population is assumed to disperse to neighboring sites and sites differ in their susceptibility to colonization (Auld & Coote, 1990). Harding *et al.* (2006) seek an understanding of invasions in patchy habitats through metapopulation theory. They conclude that, for species surviving in a landscape as a metapopulation, it is critical that colonization success is higher than the extinction rate of subpopulations. In a two-species metapolation model, an invader interacts and competes with a native species. A full range of behaviours is predicted based on the type of colonization and extinction function of the invader, and the type of influence of the native species.

To overcome the limitations of reaction-diffusion models, with respect to long-distance dispersal, and of integro-differential models, with respect to heterogeneous environments, Liebhold & Sharov (1998) developed a metapopulation model of stratified dispersal for Gypsy moth (*Lymantria dispar*). The model considers the population age structure, is based on a colony establishment rate, a colony growth rate, and a rate of spread determined by using the travelling wave equation (see previous section). The model has been used to predict how barrier zones reduce the rate of population spread, and predicts a 54% reduction of the spread rate if isolated colonies are eradicated. Based on this model, Sharov *et al.* (1998) optimized the use of barrier zones to slow the spread. The focus on the spreading front contributes to a better explanation of spreading and opens the door for the design of containment strategies.

Spatially explicit metapopulation models and methods for ranking management strategies hold a great promise for dealing with established metapopulations of invasive species. Both methods have been developed by Gilioli *et al.* (2008a) and applied to the conservation of amphibians. They introduced patch quality and influencec of between-patch landscape features into independent metapopopulation models for the amphibians *Rana temporaria* and *Bufo bufo* in a relatively closed area along the Rhine river in the Canton of the Grisons, Switzerland (Fig. 3). An incidence function model (IFM) represents the dynamics of occupied and unoccupied sites. The work aims at species conservation rather than invasive species management, but illustrates the both the development of an IFM for binomial distributions and an innovative method for the ranking of management strategies.

CONCLUDING REMARKS

A wide range of models is developed and used for study and management of invasive species. Ecologist are aware that they deal with complex systems and hence, are advised to apply complementary models (Jørgensen, 2002). For example, modelling tools designed for representing potential spatial distributions can be complemented with spread models once the invasion has taken place. As subsequently shown, the brief review provides some guidance for model selection.

In the area of risk identification and potential distributions of invasive species (Fig. 1), three tools are used. The first tool exclusively takes into account the climatic requirements of the invasive species, the second tool focuses on the population ecology and management, while the third tool considers them as members of communities and applies ecosystem methods to their study and management. The first tool makes efficient use of scarce data, the selection of the second tool may be motivated by an interest in population management, while the third method may be preferred for the assessment of effects on biodiversity and ecosystem evolution, structure and functioning.

In the area of the analysis of risk treatment options and containment design (Fig. 2), ecologists also rely on a wide range of different methodologies. Some tools meet the mean-field assumption, other tools appear to be suitable for low density populations and high biological and environmental variability, while others take into account spatial heterogeneity and fragmented landscapes. In many cases, ecologists may feel comfortable with the mean-field assumption. If not, they may have to decide between tools that are suitable for homogeneous or heterogeneous environments. If the circumstances force them to identify tools for heterogeneous environments, they may first consider the applicability of individual-based models. These models may be particularly appropriate

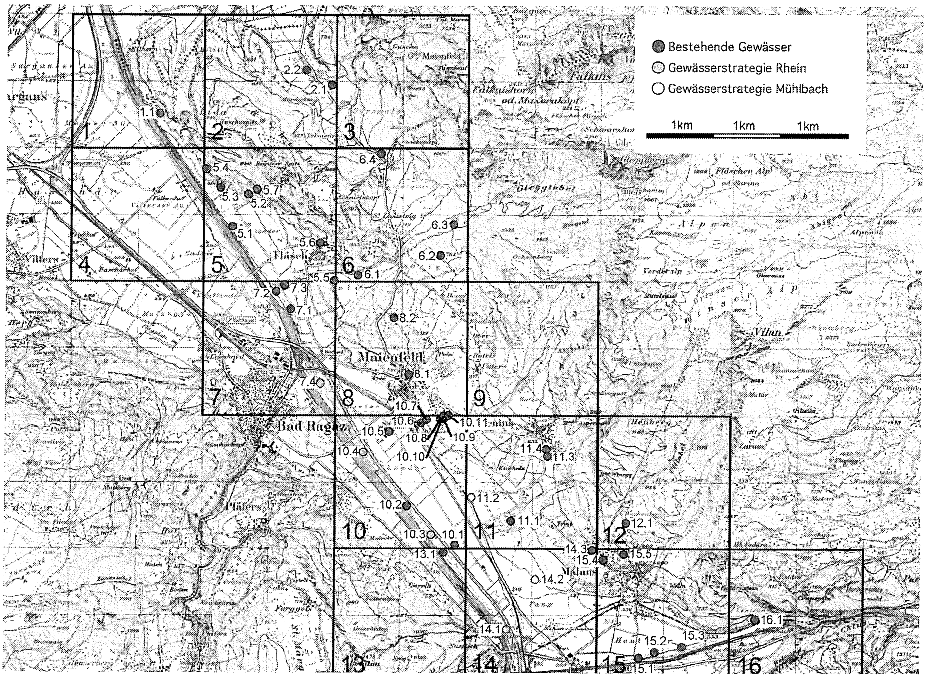

Fig. 3 - Illustration of a metapopulation model and the search for adequate management strategies: amphibian conservation in the Bündner Herrschaft (Canton, of the Grisons, Switzerland). The area is subdivided into 16 strata, red dots ''bestehende Gewässer') represent the location of existing breeding sites, pink dots ('Gewässerstrategie Rhein') represent the planned sites along the Rhine river, and yellow dots ('Gewässerstrategie Mühlbach') represent planned sites on agricultural land. Setting-up four sites along the Rhine river is a better conservation strategy than setting-up two additional sites in intensively used agricultural land (Gilioli *et al.*, 2008a). Map reproduced with permission from *Animal Conservation* and *Swisstopo*, Wabern, Switzerland.

for representing low densities of invader as observed, for example, at the beginning of an invasion. For firmly established species at relatively high densities, ecologists may choose between grid-based (lattice) and spatially explicit metapopulation models. The second approach is appropriate if the landscape is fragmented.

In general, the selection of modelling tools depends on the quality of the ecological system under study and management, as well as on the objectives to be met. In general, modelling tools are not seen as an end-product of a project (Hilborn & Mangel, 1997), but models are continuously changed in response to new information and needs. In this context, ecologists may be guided first by available data, project needs and by the criteria of intelligibility referring to the he degree to which an ecological system is intelligible, i.e. capable of being understood. For example, Gilioli *et al.* (2008b) relied initially on readily available information and opted for a tool with high intelligibility but kept the door open for the integration of better parameter estimates and for revisions of the model (Gilioli *et al.*, 2008b). In agreement with Peterson *et al.* (1997), Gilioli *et al.* (2008a, 2008b) recommended to develop the modelling tools in an adaptive management context.

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