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From data to decision – Learning by probabilistic risk analysis of biological invasions

Ullrika Sahlin



Doctoral Thesis
Department of Biology
Lund University
2010

A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case, the introductory part constitutes the formal thesis, which summarizes the accompanying papers. These have either already been published or are manuscripts at various stages (in press, submitted or in ms).

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Till mormor Brita

Psychohistory depends on the idea that, while one cannot foresee the actions of a particular individual, the laws of statistics as applied to large groups of people could predict the general flow of future events. Asimov used the analogy of a gas: an observer has great difficulty in predicting the motion of a single molecule in a gas, but can predict the mass action of the gas to a high level of accuracy. Physicists know this as the Kinetic theory. Asimov applied this concept to the population of his fictional Galactic Empire, which numbered a quintillion. The character responsible for the science's creation, Hari Seldon, established two axioms: 1) that the population whose behaviour was modeled should be sufficiently large and 2) that the population should remain in ignorance of the results of the application of psychohistorical analyses. There is a third underlying axiom of Psychohistory, which is trivial and thus not stated by Seldon in his Plan: 3) that Human Beings are the only sentient intelligence in the Galaxy. [Wikipedia, February 2010]

CONTENTS

List of papers.....	7
Svensk sammanfattning	8
1 Introduction	10
2 Background	11
2.1 Why biological invasions	11
2.1.1 Three reasons to predict futures in ecology... ..	11
I. Preserve biodiversity.....	11
II. Protect biosecurity	11
III. Reduce impact from climate change	11
2.1.2 ...with a commonality.....	12
2.1.3 Managing biological invasions	13
2.2 Predicting with uncertainty.....	16
2.2.1 Risk analysis	18
2.2.2 The “E” in risk analysis	19
2.2.3 The “P” in risk analysis.....	20
2.3 Decision making under uncertainty.....	22
3 Research process.....	23
3.1 Scientific perspective	23
3.2 Study object: probabilistic risk analysis of biological invasions.....	24
3.3 Conceptual model and major endpoints	24
3.4 Methods studied	26
3.4.1 Probabilistic models.....	26
3.4.2 Bayesian approach	26
3.4.3 Information theoretic approach.....	27
4 My research contributions	28
4.1 Outline of studies.....	28
4.2 Probabilistic risk analyses of establishment success	29
4.3 Establishment success of signal crayfish.....	33

4.4 What uncertainty to expect in the distribution of an invading population.....	36
4.5 The value of species traits as predictors of invasion success.....	38
4.6 Robust prevention and control of an invaded system.....	40
4.7 Summary of my research contributions.....	42
5 General discussions.....	43
5.1 The interpretation of probabilistic output for different strengths of background information.....	44
5.2 From data to information through the eyes of a probabilistic model.....	47
5.3 From information to decision ... and back again	48
6 Final Remarks.....	50
Tack/Acknowledgements	51
References.....	52

LIST OF PAPERS

- Paper I Probabilistic analysis of establishment success – a snapshot of models and Bayesian implementation. Ullrika Sahlin and Stefan Andersson. Submitted
- Paper II Time to establishment success for introduced signal crayfish in Sweden – a likelihood for censored data. Ullrika Sahlin, Henrik G. Smith, Lennart Edsman and Göran Bengtsson. Submitted
- Paper III When uncertainty in range expansion is shaped by landscape heterogeneity. Ullrika Sahlin, Göran Bengtsson, Henrik G. Smith. Submitted
- Paper IV A benefit analysis of screening for invasive species – base-rate uncertainty and the value of information. Ullrika Sahlin, Tobias Rydén, Cecilia D. Nyberg, Henrik G. Smith. Submitted
- Paper V Towards a robust strategy of prevention and control of biological invasions into an invaded system. Ullrika Sahlin, Jörgen Ripa, Tobias Rydén and Henrik G. Smith. In ms

The participation of the author in the papers:

Paper I: I did the literature search, compilation and classification of the probabilistic models.

Paper II: I specified the model, worked out the method together with H.G. Smith.

Paper III: I specified the spreading model and the landscape model (with participation of H.G. Smith) and worked out the method for the remaining analyses.

Paper IV: I specified the framework for benefit analysis with help of T. Rydén.

Paper V: I developed the model in cooperation with T. Rydén and J. Ripa and collected the data.

In all papers I was involved in the planning, I did all data analysis and modelling, I produced the first draft of the manuscript and finished the writing in cooperation with the co-authors.

SVENSK SAMMANFATTNING

Tre skäl till att man behöver förutsäga framtiden av ekologiska system är att bevara biologisk mångfald, upprätthålla biosäkerhet och att minska negativa effekter av en klimatförändring. Utmaningen består i att på ett vetenskapligt trovärdigt sätt göra förutsägelser om framtiden för att forma lösningar på dessa problem. Genom att beskriva osäkerhet i form av sannolikheter – med probabilistiska metoder – kan man göra förutsägelser om framtiden på ett strukturerat och åskådliggörande sätt. Med syfte att bringa klarhet i vad det innebär att göra förutsägelser om framtiden baserat på vetenskaplig kunskap har jag studerat hur man gör sannolikhetsbaserade (probabilistiska) riskanalyser av biologiska invasioner.

En av svårigheterna är att empiriska data som skall utgöra underlag för förutsägelsen saknas, eftersom det som skall studeras inte har hänt eller eftersom det som studeras innebär något nytt. Exempel på sådana osäkra förutsägelser är vad som kommer följa av ständigt pågående introduktioner av främmande arter. Man vill gärna kunna förutse vilka arter som blir ett problem, men eftersom empiriska data saknas behöver förutsägelser delvis bygga på subjektiva bedömningar av sannolikheter. Dessutom saknas det kunskap – eller råder osäkerhet om – de processer som leder fram till att en del främmande arter blir skadliga för miljö, hälsa och ekonomi.

Jag har klassificerat befintliga probabilistiska modeller av etableringsframgång hos introducerade populationer av främmande arter. Jag fann att etableringsframgång antingen beräknas som en sannolikhet för att en art lyckas etablera en population efter introduktion, eller beräknas som den tid det tar för detta att ske. Man kan dessutom välja att titta på etableringsframgång för enskilda arter eller för flera arter i ett och samma system. En händelse som skall förutsägas beskrivs på olika sätt och baseras på olika typer av tillgänglig data – för varje kombination krävs en viss probabilistisk modell.

När man har valt en probabilistisk modell som binder samman tillgänglig empirisk data med det som skall förutsägas uppstår information. Jag fokuserar på information i form av den så kallade likelihood-funktionen. I min avhandling visar jag hur denna information förekommer som ett verktyg i informationsteoretiska metoder – för att välja bra probabilistiska modeller – och i Bayesianska metoder – för att beskriva osäkerhet. Bayesianska metoder kan dessutom hantera subjektiva beskrivningar av osäkerhet vilket är nödvändigt när man saknar empirisk data. I ett av mina arbeten visar jag hur en modell kan värderas utifrån de beslut som förutsägelser skall användas till, genom att beräkna värdet av information. På detta sätt beräknade jag värdet av data på artgenskaper hos marina

makroalger, tänkt att användas till omfattande screening av potentiellt invasiva alger.

Jag har specificerat probabilistiska modeller för att beskriva osäkerheter i olika steg av en invasionsprocess. Jag har visat att mindre än hälften av introduktioner av signalkräfta i Sverige har lett fram till en lyckad etablering inom fem år efter första introduktion. Jag har visat att det i Östersjön under 1900-talet har etablerats en ny främmande art vartannat till vart tredje år. Om man tänker sig att nya arter fortsätter introduceras i samma takt behöver samhället satsa resurser på att ta bort effekterna av de arter som är etablerade och förhindra att nya etableringar äger rum. Detta är lättare sagt än gjort.

Avhandlingen heter ”från data till beslut” för att betona att förutsägelser av framtiden blir meningsfulla först i ett beslutssammanhang. Eftersom osäkerhet kan vara såväl stokastisk som kunskapsbaserad, spelar beslutsfattarens värdering av dessa in på hur förutsägelser skall framställas. I ett av mina arbeten undersöker jag hur beslut förändras när kunskapsbaserad osäkerhet tas i beaktande. I det fallet använde jag mig utav probabilistisk modellering som beskriver osäkerheten i hur ett system förändras över tiden. Jag modellerade hur antalet etablerade arter i en ekologisk region påverkas av de åtgärder man gör för att minska negativa effekter av främmande arter.

Under avsaknad av data kan man ändå beskriva osäkerhet genom att resonera kring vilken typ av probabilistisk modell som skulle kunna passa för den ännu ej observerade händelsen. Efterhand som mer empirisk data blir tillgänglig kan man låta den beskrivna osäkerheten övergå från att vara helt subjektiv till mer och mer (empiriskt) kvantitativ. I ett av mina arbeten använder jag mig utav simuleringar för att komma fram till en probabilistisk modell som beskriver de observationer jag ännu inte har gjort. Jag visar hur osäkerhet i, och även risk relaterad till, spridningshastighet av en population är känslig för hur lämpligt habitat är utspritt längs med vägen.

Att kunna göra bra förutsägelser om framtiden och dess osäkerhet är en av förutsättningarna för att finna bra lösningar på de problem ekologiska system står inför.



1 INTRODUCTION

The aim of this thesis is to shed more light on the art of predicting futures in ecology (Clark *et al.* 2001, Coreau *et al.* 2009) with the purpose of decision making under uncertainty. The starting point of my thesis coincided with the publication of two special issues in scientific journals; one in Risk Analysis, on what theoretical ecology can do for risk analysis of biological invasions (Anderson *et al.* 2004) and one in Reliability Engineering & System Safety, on how to represent uncertainty in risk analysis (Helton 2004). These special issues illustrated that risk analysis of biological invasions is a field still in progress for which methods, models and scientific knowledge are continually being produced. At the same time as there is an ongoing mission to improve how we consider uncertainty in relation to risk. The combination of science and uncertainty raises interesting questions on principles for decision making under uncertainty. For example, in the seminal book Risk and Rationality, Shrader-Frechette (1991) discusses the scientific approach to assess environmental risks and suggests methodological reforms to make risk analysis both rational and objective. Ten years later the same philosopher published a paper on the problems with the scientific method used when assessing biological invasions, such as the lack of a firm definition of a non-indigenous species, the flaws in the dominant ecological theory to predict invasions and the lack of empirical generalizations that predict which species that become invaders (Shrader-Frechette 2001). To me the role of science and how to approach scientific knowledge emerged not only as important, but also necessary, to discuss before producing any ready to use tools for risk analysis as asked for by the Swedish Environmental Protection Agency (Naturvårdsverket). Thus the synthesis provided in this thesis contributes to the progress in methodologies to be applied in future risk analyses of biological invasions.

2 BACKGROUND

2.1 Why biological invasions

2.1.1 Three reasons to predict futures in ecology...

I. Preserve biodiversity

Arguments to why we should preserve biodiversity are of different kinds relying on biodiversity having an instrumental value for human well being or as having an intrinsic value (Persson 2008). The Millennium Ecosystem Assessment (2005), conducted with the aim to provide a scientific state of the art, concludes that “biodiversity contributes directly (through provisioning, regulating, and cultural ecosystem services) and indirectly (through supporting ecosystem services) to many constituents of human well-being, including security, basic material for a good life, health, good social relations, and freedom of choice and action”. Biodiversity loss receives attention on both national and global political agendas such as the Convention on Biological Diversity (CBD 2010), which today has been approved by 193 parties (countries). The year 2009 was the first year biodiversity loss was considered as one of the global threats to the world economy (Global risk assessment World economic forum 2009). The threat statuses of species are continuously being assessed by the World Conservation Union (IUCN).

II. Protect biosecurity

Biosecurity (FAO 2010) is a holistic concept of direct relevance to the sustainability of agriculture, food safety, and the protection of the environment, including biodiversity. It is “a strategic and integrated approach that encompasses the policy and regulatory frameworks ... that analyse and manage risks in the sectors of food safety, animal life and health, and plant life and health, including associated environmental risk”.

III. Reduce impact from climate change

Most climate scientists agree that the rate of increase in CO₂ and higher temperatures are caused by human activities since the dawn of industrialization (IPCC 2007b). The negative impacts associated with a changing climate may change ecosystems structure and functioning which may inhibit the delivery of ecosystem services (IPCC 2007a). Future

changes of ecosystems are being predicted based on climate scenarios (IPCC 2007b).

Box 1. Definitions used by CBD.

(<http://www.cbd.int/> January 2010)

Alien species - refers to a species, subspecies or lower taxon, introduced outside its natural past or present distribution; includes any part, gametes, seeds, eggs, or propagules of such species that might survive and subsequently reproduce.

Invasive alien species - means an alien species whose introduction and/or spread threaten biological diversity.

Introduction - refers to the movement by human agency, indirect or direct, of an alien species outside of its natural range (past or present).

Intentional introduction - refers to the deliberate movement and/or release by humans of an alien species outside its natural range.

Unintentional introduction - refers to all other introductions which are not intentional.

Establishment - refers to the process of an alien species in a new habitat successfully producing viable offspring with the likelihood of continued survival.

2.1.2 ...with a commonality

A problem related to all these three issues above is the introduction of non-indigenous species leading to harmful biological invasions. A biological invasion (Box 1) is the process where a species is introduced into an area where it did not exist before, establish a population, expand its range and interact with the new community (Mack *et al.* 2000). Not only have introduced non-indigenous species had negative impacts on health and socio-economic values (Pimentel *et al.* 2001, 2005) – they are also considered as potential drivers of the problems mentioned above. Biological invasions are regarded as a major threat to biodiversity (Sala *et al.* 2000). Article 8(h) of the CBD (CBD 2010) states that “each contracting party shall, as far as possible and as appropriate, prevent the introduction of, control or eradicate those alien species which threaten ecosystems,

habitats or species”. Biosecurity aims at preventing “the introduction of plant pests, animal pests and diseases, and zoonoses, the introduction and release of genetically modified organisms (GMOs) and their products, and the introduction and management of invasive alien species and genotypes”. The act of deliberately introducing harmful species as an act of bioterrorism adds another aspect to biosecurity (Meyerson and Reaser 2003). Climate change is believed to increase the threat posed by non-indigenous species for example by facilitating the spread of harmful non-indigenous species (IPCC 2007a, Walther *et al.* 2009).

Many introductions have occurred during 20th century (Hulme 2009) and since there often are time lags between the introduction and the impact of an introduced species, the problem with biological invasions is expected to increase in the future. Thus, predicting the outcome of biological invasions is highly relevant if we are to take measures before it is too late. What to predict is to be understood from a management perspective of biological invasions and I therefore continue with a brief introduction to this subject.

2.1.3 Managing biological invasions

Management of biological invasions are generally divided into early detection, prevention and control (McNeely *et al.* 2001). Early detection makes it possible to stop potentially harmful species from being introduced (Mack *et al.* 2000), with different approaches depending on if introductions are intentional or unintentional (Box 1). Prevention implies allocation of resources to stop events that already have a low probability of occurring, while measures for control are both low in success and costly for those species that already have established self-sustaining populations in the new system (Simberloff *et al.* 2005). Most non-indigenous species are not a problem (Williamson 1999). On the contrary many of the introduced species are beneficial in agriculture, aquaculture, forestry, horticulture and recreation (Gozlan and Newton 2009). All non-indigenous species should therefore not be regarded as a problem per se. However, those species that become problematic are difficult – and most often impossible – to eradicate once established, with potentially irreversible effects as a consequence (NRC 2002). Predicting which species that will become harmful (invasive) if introduced therefore constitutes a major task in the management of biological invasions (McNeely *et al.* 2001, Lodge *et al.* 2006). Predictions are suggested to be based on species traits as well as similarities found by climate matching (NRC 2002, Stohlgren and Schnase 2006). Despite considerable efforts to find predictors among species traits, the few robust predictors over taxonomic groups are propagule pressure, climate match and invasion history (Hayes and Barry 2008).

Because of large uncertainties in the outcome of introductions and the management alternatives, strategies for managing biological invasions often advocate that decisions should be based on risk analysis (McNeely *et al.* 2001, Lodge *et al.* 2006, Hulme *et al.* 2009). In particular, the quality of predictions plays a role when management call for controversial actions, such as the trade-off between preventing potentially harmful species to be introduced and free trade (Cook and Fraser 2008). Predicting potential problem species (Kolar and Lodge 2001), hot spots for invasions (Drake and Lodge 2004) and the mechanisms driving invasions (Hulme 2009, Hulme *et al.* 2009) are not only important in order for management to be effective, but also necessary for management to be accepted by the society.

Another difficulty lies in the evaluation of impacts, which could be both negative and positive. The ecological impacts from non-indigenous species are found on several biological levels ranging between individual, population, community and ecosystem levels, and effects can be both direct and indirect (NRC 2002). By, so called, invasive non-indigenous species some mean those that spread fast and become abundant, while others mean that they are species with harmful effects in the new system (Falk-Petersen *et al.* 2006). The rate of spread is not enough to predict species' impact (Ricciardi and Cohen 2007) and there is a need to quantify impact by the effects on values that are to be protected and consider expanded range or population size (Parker *et al.* 1999). Impact on biodiversity has been estimated by the number of native species threatened by non-indigenous species (EEA 2004, Berglund 2009), but this requires consideration of threats other than biological invasions and the possible synergistic effects among these (Brook *et al.* 2008). Counts of the number of non-indigenous species provide another possibility to assess the status of biological invasions (McGeogh *et al.* 2006), but the actual impact is dependent on whether the cumulative effect from multiple non-indigenous species are synergistic, independent or antagonistic (NRC 2002, Ricciardi and Kipp 2008). Economic impacts have been assessed in monetary terms (Pimentel *et al.* 2001, Pimentel 2005, Kettunen *et al.* 2008, Gren *et al.* 2009), but this holds substantial challenges for economic methods (Nunes and Markandya 2007, Carlsson and Kataria 2008) to be able to include non-market values such as aesthetical ones.

Not only is the outcome of introduction of a non-indigenous species uncertain, we are also uncertain in how uncertain this outcome is. Risks associated with biological invasions are, together with new technologies such as genetically modified organisms, so called uncertain risks (explained below). Therefore uncertainty is the major theme in my thesis and below I expand what it means to predict with uncertainty.

Box 2. Different ways to predict.

(after Peters and Herrick 2004, Coreau *et al.* 2009).

Extrapolation - to extend the spatial extent or refine the resolution of measured data to arrive at a broader scale or finer grained estimate

Forecast - the best projection or prediction about the future given by one particular model or one particular expert (e.g. weather forecast). Clark *et al.* (2001 Science) defines ecological forecasting as “the process of predicting the state of ecosystems, ecosystem services, and natural capital, with fully specified uncertainties, and is contingent on explicit scenarios for climate, land use, human population, technologies, and economic activity.”

Foresight - a construction about the future, with the aim to prepare for it. There is a strong link with management and decision making (e.g. technology foresight).

Prediction - a statement about what is thought will happen in the future, often associated with probability distributions. The main characteristics of future predictions are their degree of certainty, which lead to only one prediction (compared to the multiplicity of scenarios). Many authors use the term prediction to describe the result of a modelling exercise based on a set of assumptions. For example, Peters and Herrick (2004) let predict be “to declare or indicate in advance, to foretell on the basis of observation, experience or scientific reason”, by the motivation that general definition is preferred when common usage makes a stricter definition unnecessary and confusing.

Projection - a statement about what would happen, based on the extrapolation of past and current trends (e.g. population projections).

Scenario - a plausible description about alternative futures, based on a coherent and internally consistent set of assumptions about key relationships and driving forces.

Storyline - a coherent story (narrative) about what may happen in the future.

2.2 Predicting with uncertainty

There are several ways to produce predictions of futures states (Box 2). What to predict may be the result of a dialogue between policy-makers, managers, and the general public (Clark *et al.* 2001). The ability to predict may be challenged by uncertainties (Box 3) in how we perceive and express the states of systems (Halpern *et al.* 2006). How uncertainty is dealt with depends on the purpose of predictions (Kinzing *et al.* 2003). When the goal is to describe the world, as in traditional science, strategies dealing with uncertainty are developed to protect against being wrong. When the goal is making good decisions, as in policy making, uncertainty are dealt with aiming for accuracy.

Box 3. The meaning of uncertainty.

Uncertainty can be broadly classified into **epistemic** uncertainty (uncertainty in determinate facts) being measurement error; systematic error; natural variation; inherent randomness; model uncertainty; and subjective judgment, and **linguistic** uncertainty (uncertainty in language) being vagueness, context dependence, ambiguity, indeterminacy of theoretical terms, and underspecifity (Regan *et al.* 2002).

Some chose to let epistemic uncertainty be separated from uncertainty being **stochastic** (aleatory) (Paté-Cornell 1996, Bedford and Cooke 2001). Stochastic uncertainty arises from variability in the system and can be quantified from data using statistical methods or by expert judgment, while the remaining epistemic uncertainty (state of knowledge) can only be quantified by experts (Bedford and Cooke 2001). However, the distinction between epistemic and stochastic uncertainty is not sharp and depend the particular model and purpose of prediction. For example, one can choose to model the average behaviour of a population instead of the behaviour of each individual. Schultz (2008) distinguish between data uncertainty resulting from information being inconclusive, incomplete, or non-existent, and methodological uncertainty involving disagreement over which methodologies or models that are most appropriate or reliable to use.

Kinzing *et al.* (2003) pointed out four difficulties in the encounter of science and decision making related to the different ways to deal with uncertainty. First, uncertainty may not be properly communicated. The success of a prediction depends on the accuracy of estimations and the communication of information and uncertainty (Regan *et al.* 2005b). Second, what is useful uncertainty may be different for scientists and decision makers. Trying to reduce uncertainty, scientists tend to avoid complex ecological systems or use methodologies that remove uncertainties that are not of interest to the scientific question. However, it may be just these systems that are of interest for the decision makers (Kinzing *et al.* 2003). Missing important sources of uncertainty can result in predictions appearing to be less uncertain than what they actually are e.g. having too narrow confidence intervals (Clark *et al.* 2001), or not including extreme or rare events (Ludwig 1996). Third, difficulties to quantify uncertainty may result in avoidance of uncertainty in predictions and scientists may feel uncomfortable expressing how likely something is to occur. Four, there is no such thing as objective science (see also Shrader-Frechette 1991) – the values of scientist influence the scientific output. In fact, scientific work on biological invasions is full of value laden and subjective judgment, such as whether non-indigenous species pose a threat to native ecosystems or not (Larson 2007).

The failure of management strategies due to missed important uncertainties in predictions is not good for the trust in science, managers or decision-makers (Clark *et al.* 2001, Regan *et al.* 2005a). Focus need to be directed on the causes of uncertainty, e.g. mechanisms for long-distance dispersal of an invading population (Clark *et al.* 2001), and on how to address and communicate uncertainties when predicting. A scientifically based predictive system should be transparent, open to review and evaluation by experts, rest on a logical framework and be repeatable (NRC 2002). Predicting with uncertainty can therefore be approached by risk analysis which is meant to provide information for decision resting on scientific principles and best knowledge (NRC 2002, Aven and Kristensen 2005).

Box 4. Some useful definitions related to risk analysis.

The definitions is taken from Aven (2003) who unless stated otherwise use the ISO (International Organization for Standardization) standard.

Risk – uncertainty of the performance of a system (the world), quantified by probabilities of observable quantities.

Probability – a measure of the uncertainty of an event. According to ISO it is defined as “the extent to which an event is likely to occur”.

Observable quantity – quantity expressing a state of the world that is unknown at the time of the analysis but will, if the system being analyzed is actually implemented, take some value in the future, and possibly become known.

Risk analysis – systematic use of information to identify sources and assign risk values.

Risk evaluation – process of comparing a risk against given risk criteria to determine the significance of the risk. Risk evaluation may be used to assist the decision making process.

Risk management – coordinated activities to direct and control an organization with regard to risk.

2.2.1 Risk analysis

Risk analysis is a tool to predict outcomes while considering uncertainty in both the system and in our knowledge of the system (Box 4). A risk analysis seeks the answers to the triplet questions:

What can go wrong?,
How likely is it? and
What are the consequences?,

with the purpose to show how the risk changes under different decision alternatives. Risk is in itself a combination of the likelihood and consequences of an undesired event (Kaplan and Garrick 1981, Aven and Kristensen 2005). In this thesis I interpret likelihood in the definition of risk as the probability of the undesired event.

The use of the terms risk analysis and risk assessment is confusing. The ISO standard regards risk assessment as the overall process of risk analysis and risk evaluation (Aven 2003), while others define risk assessment as part of risk analysis; CBD (2010) use risk analysis referring to: (1) the assessment of the consequences of the introduction and of the likelihood of establishment of an alien species using science-based information (i.e., risk assessment), and (2) to the identification of measures that can be implemented to reduce or manage these risks (i.e., risk management), taking into account socio-economic and cultural considerations. The Society for Risk Analysis (SRA 2010) defines risk analysis broadly “to include risk assessment, risk characterization, risk communication, risk management, and policy relating to risk”. The beauty in the terminology is perhaps best captured by Burgman (2005) who views risk analysis as the “evaluation and communication of the nature and extent of uncertainty” and risk assessment as the “completion of all stages of the risk management cycle, a marriage of risk analysis methods, adaptive management, decision tools, monitoring and validation”.

2.2.2 The “E” in risk analysis

Non-indigenous species can be seen as a “biological pollution” (Olenin *et al.* 2007), and risk analysis of biological invasions is a sort of Environmental risk analysis considering both Ecology and Epidemiology. Suter (1993) defines an ecological risk analysis as “the process of evaluating the potential for adverse ecological effects that may occur as a result of exposure to contaminants or other stressors”. Stressors can be chemical, physical or biological (US EPA 1998) such as toxic chemicals, pesticides, nutrient enrichment, ozone depletion, harvesting, habitat loss, natural disasters, climate change, genetically modified organisms, but also introduced non-indigenous species (US EPA 1998, Chapman 2002). Adverse ecological effects are measured on several biological levels ranging from the mortality of single organisms to loss of ecosystem functions (US EPA 1998). The impacts from biological invasions are not purely ecological, but also encompass effects on human health and economy (Mack *et al.* 2000). Environmental risks are typically assessed by analyses of exposure and effects (US EPA 1998, McCarty and Power 2000). The third E comes from Epidemiology highlighting that a biological stressor which, as opposed to a chemical or physical one, reproduces and spreads in the new system. This requires other types of approaches, e.g. with a process perspective, for risk analysis (Mollison 1986, US EPA 1998).

2.2.3 The “P” in risk analysis

In one way risk analysis is about Predicting using Probabilities. The challenge for risk analysis of biological invasions is to make predictions in a complex system suffering from scientific uncertainty (Leprieur *et al.* 2009) despite sparse empirical data or similar historical events. As a consequence, risk analyses of biological invasions are most often qualitative (Hayes 1997). However, since such analyses often suffer from subjective flaws and are poor in handling uncertainty (Burgman 2000), methods for risk analysis should rather be quantitative. A quantitative approach is provided by probabilistic risk analysis which has originated from the nuclear, aerospace and chemical process sectors to predict events “that (almost) never occurs” (Bedford and Cooke 2001). Probabilistic (or quantitative) risk analysis may provide the transparent and rigorous quantification of uncertainties asked for by policymakers (NRC 2002). Probabilistic analysis offers a method being transparent since “once there is a model, only accepted rules of probability take us from data to inference to prediction” (Clark 2005), and rigorous for example by forcing us to specify our knowledge through the use of probabilistic models.

Using probabilities to quantify uncertainties pose new demands on the risk analysis. The first thing to consider is that any measure of probability will not be able to describe all types of uncertainty (Bedford and Cooke 2001). For example, linguistic uncertainty (Box 3) can lead to violations of the basic rules of probability (Colyvan 2008). The foundation of the probability measure is build upon a few axioms (Kolmogorov 1956) and, for example, when events are defined by vague or ambiguous terms, the probability of an event and the negation of this event do not necessarily sum up to one (Colyvan 2008). One recommendation is to let methods to address linguistic uncertainties forego a probabilistic risk analysis (Burgman 2005). Other chooses to relax some of Kolmogorov’s axioms and quantify uncertainty by non-probabilistic measures such as imprecise probabilities, fuzzy logic and intuitionistic logic (Helton 2004, Burgman 2005, de Rocquigny *et al.* 2008). This thesis focuses on probabilities as the only measure of uncertainty.

A second consideration when performing probabilistic risk analysis is how to handle uncertainty of various strengths of scientific evidence. For example, risk analysis of biological invasions needs to address information ranging from planned experimental results, peer reviewed journal data, grey literature data to unstructured expert opinion (Keith Hayes personal communication). When empirical data is unattainable, uncertainty can be quantified based on expert judgements. Probability distributions for parameters can then be produced by letting the experts themselves produce

a consensus probability distribution or by aggregating the experts' individual probability distributions after their elicitation (Bedford and Cooke 2001). Whether the quantification of uncertainty has been objective or subjective (or both) is important for a decision-maker. Subjective judgments of probabilities tend to be biased on individuals' perception (Tversky and Kahneman 1974, Burgman 2000). On the other hand subjectivity does display preferences over risk, which motivates why risk analysis should strive to be a democratic process involving the opinions of stakeholders, i.e. those affected by the risk (Shrader-Frechette 1991).

A third consideration is the interpretation of probability. Probability can have different meanings (Cox 1946, Bedford and Cooke 2001); it can express the true probability that something will occur (the classical view), the relative frequency given a large enough sample (the frequentist view) or our degree of belief about the occurrence of a future event (the subjective view). The interpretation of probability becomes important when the risk analysis is handed over to a decision maker. Risk analysis in practice is more or less influenced by subjectivity (Regan *et al.* 2005b). Further, decision makers may have different attitudes towards risk, ranging from being averse, over neutral to prone towards risk. In the same way can decision maker have an attitude towards uncertainty (see e.g. Akcakaya *et al.* 2000). Decision-making involves not only assessing the risk but also to state once preferences over risk, for example, establishing acceptable levels of risk (Shrader-Frechette 1991). A risk analysis should work as a tool for decision support even under subjective quantification or large epistemic uncertainty (Box 3). Therefore there is (or should be) a close link between what framework we choose for the presentation of uncertainty and on what basis (rationality) decisions are made (de Rocquigny *et al.* 2008, Aven 2010). Frameworks of ecological risk analysis distinguish more or less between science and policy, dependent on whether the focus is on the assessment of risk or the social dimension on risk (McCarty and Power 2000). It is important to highlight the meaning behind uncertainty for those providing the information and for those making decisions. What strategy to use in policy making is affected by the occurrence of risk events, the magnitude and perceptions of consequences and the extent of uncertainty (Klinke and Renn 2002) Even though this thesis is about predicting the future of uncertain ecological systems it has become inevitable to not involve the decision making process, which I briefly introduce in the next section.

2.3 Decision making under uncertainty

Decision theory can be both normative, how decisions should be done, and descriptive, how decisions are done. There is a difference between decisions made under risk and decision made under uncertainty (Hansson 1999), or in other words, under first and second order uncertainty (Gärdenfors and Sahlin 1982). In the first case probabilities to describe the risk are known, while in the second probabilities are either not known at all or only known with insufficient precision.

When making decisions under uncertainty the preferences over risk and uncertainty needs to be specified. Two prevailing approaches for decision making under uncertainty are the Bayesian approach and the minimax principle (Aven 2003, Shrader-Frechette 1991). The Bayesian approach treats all uncertainty as equal by basing decisions on an expected utility. This is risky since it ignores uncertainty in utilities and probabilities (Burgman 2005). Therefore it is desirable to separate between stochastic and epistemic uncertainty. According to the minimax principle the decision maker prefers decision alternatives with the lowest possible maximum loss and can thereby choose alternatives with a higher expected loss but a with less uncertainty. Some even go further and choose to quantify epistemic uncertainty with non-probabilistic measures (e.g. fuzzy logic, possibilities; Helton 2004, Burgman 2005, de Rocquigny *et al* 2008). The problem then becomes how to make the decisions. This is an ongoing topic, even in Ecology (see for example Regan *et al.* 2005a).

3 RESEARCH PROCESS

3.1 Scientific perspective

Scientific interest can be either descriptive or prescriptive (March and Smith 1995). Descriptive research aims at understanding the nature of, for example, ecological systems. It is a knowledge-producing activity corresponding to natural science. Prescriptive research aims at improving system performance. It is a knowledge-using activity corresponding to design science. Both scientific perspectives are relevant and depend on output from each other. For example, natural scientists produce scientific knowledge which design scientists can exploit to develop new technology, and an artefact constructed by design scientists can be used to gain more knowledge of natural laws. As one ecologist put it “the role of science in the decision-making process and the research required to develop a capability of predicting ecological futures is to provide knowledge of the system that is to be predicted but also to improve how predictions are made” (Clark *et al.* 2001). The former is a task for traditional natural science focusing on understanding the processes in the systems of interest. The latter role involves the issue to communicate uncertainties in predictions to improve decision-making, and is a task for someone with a design perspective on science.

Distinguishing between natural science and design science can easily become complicated and is, in one sense, even unnecessary. March and Smith (1995) therefore suggests to instead describe research by its outputs and activities. They categorize research outputs as constructs, model, method and instantiation (i.e. the implementation in a real setting) and divide research activities into build, evaluate, theorize and justify. The research activities to build and evaluate is most common in design science, while theorize and justify fits into natural science. I believe that adopting this broader perspective on science provides legitimacy for asking different types of questions when working with solving ecological and environmental problems and still doing science. My research is to be understood as a process where the research questions have emerged when the problems have been presented and after settling criteria for their solutions.

3.2 Study object: probabilistic risk analysis of biological invasions

The aim of this thesis is to improve the knowledge of how to predict futures in ecology with the purpose of making decisions. I have approached this aim with five studies focusing on probabilistic risk analysis of biological invasions with the purpose to identify and solve issues related to predicting with uncertainty for decision making. My research activities have been to build and evaluate models for probabilistic risk analysis related to biological invasions. My research outputs are therefore models and methods. The reasons for choosing probabilistic risk analysis of biological invasions as study object for my case studies were:

- I. The application of probabilistic risk analysis is relevant to improve risk management aiming to preserve biodiversity, maintain biosecurity or reduce the impact from climate change.
- II. There is a need to consider uncertainty both in stochastic events and determinate facts (epistemic uncertainty).
- III. There is a need to combine subjective judgment with statistical inference.
- IV. Models and methods for probabilistic risk analysis are still under development and there is a need for standards of the quantification of uncertainty.

In the following sections, I give a brief description of risk analysis of biological invasions and outline the papers included in this thesis. I continue with a cross-cutting analysis of my studies. Finally, I provide a synthesis of my findings concerning how to predict with uncertainty.

3.3 Conceptual model and major endpoints

A biological invasion can be conceptualized as a chain of event from introduction, i.e. the transport from donor to recipient system and survival in the new environment, followed by establishment and spread, finally leading to impact on human health or economic and environmental values (see the front cover of this thesis). An invasion is successful when the alien species succeed in each of these steps in the chain (Williamson 1999, Kolar

and Lodge 2001, Heger and Trepl 2003). The outcome of a biological invasion depends on a combination of factors related to traits of the invading species, abiotic and biotic conditions in both the donor and the recipient systems, and propagule pressure (Lodge *et al.* 2006, Catford *et al.* 2009).

Information on environmental matching, previous invasion history, propagule pressure, and species traits are examples of entries to target invasive species among those with a potential of being introduced (Lodge *et al.* 2006, Barry *et al.* 2008). Environmental matching and previous invasion history are used to predict invasiveness by utilizing the similarity between the environment in the native and the potential range, or between earlier and future events of invasion, respectively. Propagule pressure as a predictor of invasiveness rests on a mechanistic understanding of the invasion process, conceptualizing that a stronger introduction effort results in a higher probability to succeed. The use of species traits as predictors of invasiveness rely on the paradigm that invasive species share certain characteristics, which for instance can be specific within a taxonomic group. Even though general characteristics are difficult to find (Hayes and Barry 2008), species traits are frequently recommended and used as predictors of invasiveness (Lodge *et al.* 2006, Barry *et al.* 2008).

Risk analyses of invasions of non-indigenous species are aimed to predict the probability of one or several events in this invasion chain (Richardson *et al.* 2000, Kolar and Lodge 2002, Colautti and MacIsaac 2004) and the impacts on the ecological and socio-economical systems following a successful introduction (Leung *et al.* 2002). The prediction of species' potential to become invasive has been given considerable attention in ecological modelling, but with varying success (Kolar and Lodge 2002, Hayes and Barry 2008). The consequences following an introduction are more difficult to foresee and quantify (Lodge *et al.* 2006, Strayer *et al.* 2006). The losses resulting from introductions of invasive non-indigenous species are generally considered to be larger than the potential benefits (McNeely *et al.* 2001, Keller *et al.* 2007, Hulme *et al.* 2009), with the exception of the most common crops and cultivated species. Monetary estimates of the impact of invasive species are difficult to obtain, but nevertheless possible, using the wide array of available economic tools (Nunes and Markandya 2008).

Risk analyses of biological invasions can be categorized by their assessment endpoints. Assessment endpoints represent the values the analyst is trying to protect (Burgman 2005) but can also be the events the analyst is trying to avoid. There are five major endpoints of biological invasions: Introduction, Establishment, Distribution, Impact – species and Impact – system. The first endpoints represent steps in the biological

invasion event chain. Risk analysis with a species endpoint aims to distinguish harmful invasive species from harmless non-invasive ones. The endpoint describing the impact on an invaded system can be impact in relation to a specific non-indigenous species (e.g. Ricciardi 2003) or on the total impact in the system (e.g. Berglund 2009). The prevailing endpoint for risk analysis of a single species invasion is the probability of, or the time for, a transition from one stage to another. The prevailing endpoint for risk analysis of multi-species invasions is the intensity of endpoint events and the accumulated impact over time.

3.4 Methods studied

3.4.1 Probabilistic models

Probabilistic models can be statistical, dynamic state or Bayesian models (Aven 2003). A statistical model fits one or several probability distributions to a random variable describing the probabilistic behaviour of a quantity that can be observed, based on the existence of an underlying statistical population. Statistical models are implemented to estimate parameters in a regression or relevant characteristics of random variable, such as the mean, median or a percentile. Dynamic state (or process) models use probabilities for the transition between different states which can be discrete or continuous. Bayesian models incorporate prior information on parameters in the corresponding statistical or state dynamic model and allow empirical data to enter the analysis via the likelihood (Aven 2003).

3.4.2 Bayesian approach

A Bayesian analysis consists of a probabilistic model for a (in this example discrete) quantity Y and parameter θ denoted as $p(\text{data}, \theta)$, where the parameter is assigned a prior distribution $p(\theta)$ based on background knowledge. The posterior distribution for the parameter θ is found after updating the prior distribution with the observed data using Bayes' rule and is

$$p(\theta / \text{data}) = p(\text{data}, \theta) p(\theta) / \int p(\text{data}, \theta) p(\theta) d\theta.$$

The predictive posterior of Y , $P(Y = y / \text{data})$, is found by combining the probabilistic model and the posterior distribution on parameters and is given by

$$P(Y = y / \text{data}) = p(y, \theta) p(\theta / \text{data}).$$

– learning by probabilistic risk analysis of biological invasions

Predictions about the uncertainty in X is given by predictive posterior distribution

$$P(Y = y | data) = \int p(y, \theta) p(\theta | data) d\theta.$$

The likelihood $L(\theta | data)$ is the same as the joint probability of observing the data from Y conditional on the parameters in the probabilistic model, here denoted as $p(data | \theta)$.

3.4.3 Information theoretic approach

Based on the likelihood, the Akaike information criterion is calculated as

$$AIC = -2\ln L(\theta | data) + 2k,$$

where k is the number of parameters in θ (the probabilistic model). The Akaike weight of model i in the set of candidate models $j = 1, \dots, R$ is calculated as

$$w_i = \exp(-1/2\Delta_i) / \sum_j \exp(-1/2\Delta_j),$$

where $\Delta_i = AIC_i - AIC_{\min}$ is the Akaike difference. Sometimes only the models with an Akaike difference larger than two are considered (model selection).

The Akaike weight is used to weight the models in the candidate set after how much evidence they receive from data. The Akaike weight can also be used to produce weighted sums of models for inference or prediction (model averaging). For a more comprehensive review I refer to Burnham and Anderson 2002 and Johnson and Omland 2004.

4 MY RESEARCH CONTRIBUTIONS

4.1 Outline of studies

The first paper is a review of probabilistic models of establishment success in a sample of published articles (Paper I). I particularly ask how establishment success was defined and how uncertainty was quantified in different studies. In the second study I specified a probabilistic model of establishment success in which I addressed various methods for including covariate effects (Paper II). In the third study I modelled the uncertainty in a biological invasion endpoint as a function of two common metrics of landscape characteristics (Paper III). I derived a probabilistic model for the uncertainty in expanded range (i.e. related to the distribution endpoint) given a certain amount of suitable habitat and its degree of fragmentation for two types of dispersal behaviour of the spreading species. In Paper IV I derived the value of information on species characteristics when used to screen for potentially invasive species. The value of information was then used to estimate the benefit of a model to predict species invasiveness under different base-rates. In the last study (Paper V) I derived a robust strategy to reduce the impact from multiple-species invasions on a system, with particular emphasis on robustness to uncertainty in the dynamics of the system. Below I describe the objectives and the main results for each study (summarized in Table 1). For a detailed description of the studies I refer to the original papers appended in this thesis.

– learning by probabilistic risk analysis of biological invasions

Table 1. The studies in this thesis with respect to the studied aspect on uncertainty, biological invasion endpoint and if focus is on predicting solely or on decision making.

	Paper I	Paper II	Paper III	Paper IV	Paper V
Aspects on uncertainty	Type of probabilistic models, type of predictions, Bayesian approach	A probabilistic model for censor data considering censoring, methodology considering multi-collinearity, information theoretic approach to model selection and prediction	A model for the likelihood given information on landscape characteristics, Competing risk model, stochastic dominance, extreme value theory	Pre-posterior value of information analysis, the base-rate effect	How to include uncertainty in decision-making, epistemic uncertainty, Bayesian quantification of uncertainty
Biological invasion endpoint	Establishment	Establishment	Distribution	Impact - species	Impact - system
Major focus	Predicting risk			Risk in a decision context	

4.2 Probabilistic risk analyses of establishment success

The first two studies (Paper I and Paper II) focused on the probability of establishment success for two reasons: First, establishment success is the final step in the chain of events leading to a successful introduction (Carlton and Ruiz 2005) and represents the first event in an analysis of the biological or economic impact of non-indigenous species (the bow-tie view in Figure 1). Establishment success is therefore a common endpoint event in risk analyses of biological invasions. Second, establishment can be modelled based on mechanistic principles (Rejmanek 2000, Hayes and Barry 2008) using factors related to, for example, the intensity of introduction, the number of arriving individuals, and the chances of survival in combination with measures of reproduction success and population growth. It is therefore reasonable to expect a variety of models of establishment success emphasizing different key aspects of the invasion process.

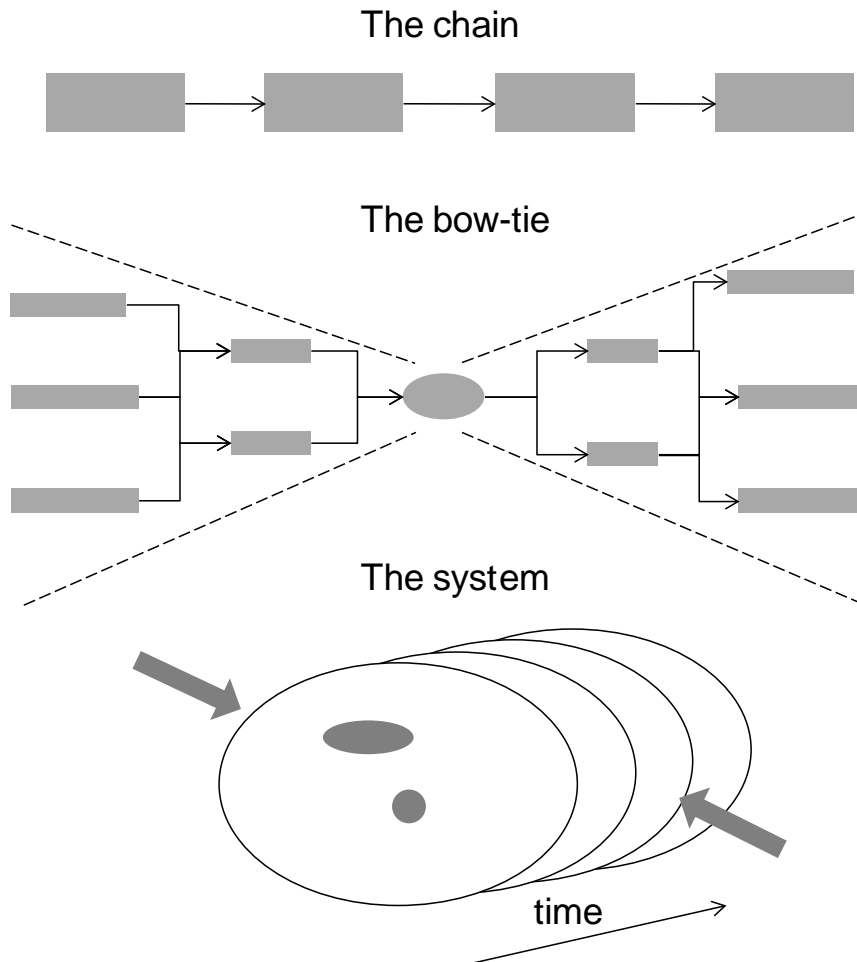


Figure 1. Three different perspectives on risk. The chain perspective places endpoint events in a chain of events where one event must happen in order for the next to occur. The bow-tie model consider the possible ways an undesired event can be initiated (e.g. a fault tree) and/or the events following an initiating event (e.g. an event tree). The system perspective is to let initiating events (threats) influence the performance of a system over time.

The survey of probabilistic models of establishment success in Paper I resulted in the classification scheme shown in Figure 1, showing different approaches to model uncertainty in establishment success. Some studies derived predictions of establishment success based on a likelihood function. In these likelihood-based predictions, empirical observations enter the analysis via the likelihood function, and risk is derived from the parameters in a probabilistic model. Other studies derived forecasting-type of predictions. In this approach, there is no data on “similar” events to base predictions on; instead one uses a deterministic or stochastic model where uncertainty in input parameters is propagated into uncertainty in predictions. A number of models were directly implemented in a decision theoretical context; in some cases, the uncertainty in predictions was expressed as a distribution of errors.

I found that establishment success was generally measured as a probability of success given introduction (transition probability) or as the time from introduction until success or failure in establishing a viable population (transition time). Time is an important confounder in establishment success. Even though time can be included as a covariate in models where establishment success is measured as a transition probability, the influence of time is given a different and perhaps more consistent treatment in models of transition time.

Establishment success was also measured at various degrees of species specificity, with some studies focusing on the establishment success for a single species introduced into one or several sites, and others dealing with the “average” establishment success for a group of species introduced into a bounded system. Establishment success was, for example, quantified at a high degree of species specificity when the purpose was to identify species with a high potential of establishing using information on species traits. Examples of establishment success at a low degree of species specificity are quantifications of a base-rate of establishment success for a randomly chosen species among a group of species in a system (see more in Paper IV) or assessments of the vulnerability of a system to invasions (Paper V). Specifying a probabilistic model of establishment requires a definition of when a population is regarded as successful in establishing. Among the various definitions, establishment success defined as the exceedence of a criterion, for example, the time to first passage of population abundance above a critical threshold is both consistent with time as an important confounder and under recurrent events of introductions.

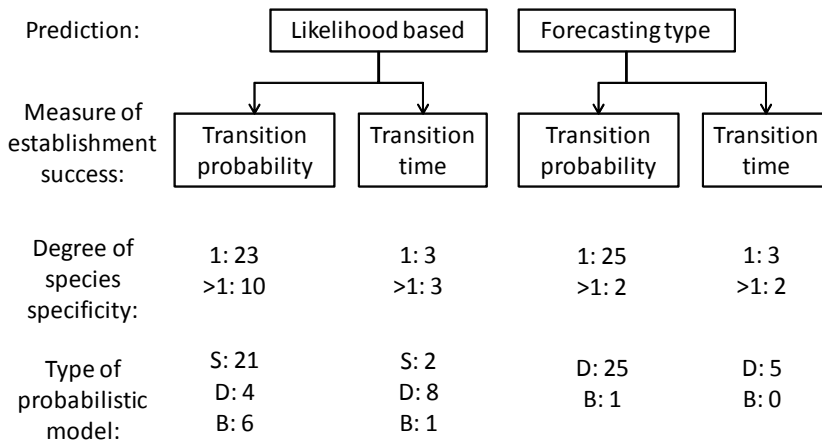


Figure 2. The classification scheme in Paper I to classify probabilistic models of establishment success after the type of prediction, measure of establishment success, degree of species specificity (the success for a single species (1) or the average success in a group of species (>1)) and type of probabilistic model (Statistical (S), Dynamic (D) or Bayesian (B)).

Predictions of establishment success must partially rely on expert knowledge and I therefore looked for explicit Bayesian approaches, which offers the possibility to base predictions on combinations of observational data and subjective knowledge (Aven and Kvaloy 2002). The second objective in Paper I was therefore to investigate the extent to which the encountered probabilistic models for predicting establishment success use — or has the potential to use — the Bayesian approach for prediction of establishment success. A majority of the published studies were based on statistical or dynamic state models while few models were explicitly Bayesian and almost all of these had been published in the past few years (Figure 3). However, many of the models in the review could be used with a Bayesian approach by, for example, adding prior distributions to parameters.

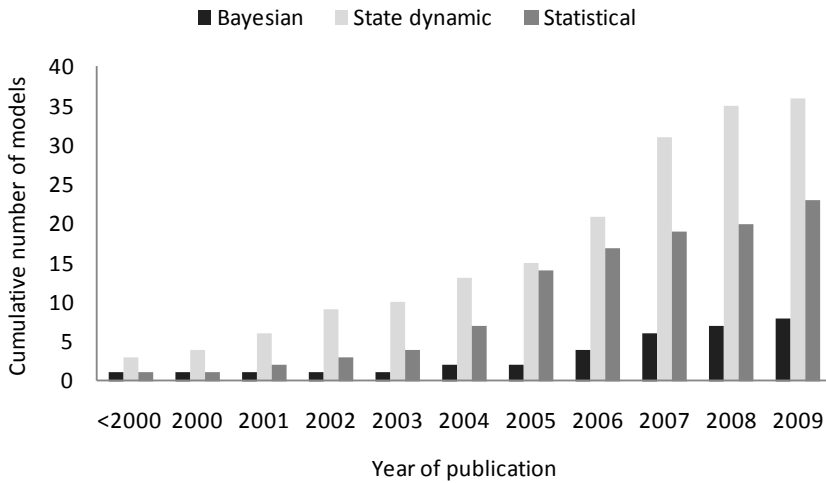


Figure 3. The cumulative number of identified probabilistic models, categorized as Bayesian, state dynamic and statistical, as a function of publication year.

4.3 Establishment success of signal crayfish

The objectives in Paper II were 1) to specify a probabilistic time-to-event model to predict the time to successful establishment of an introduced population for risk analysis, and 2) to parameterize the proposed model by using data on establishing populations of signal crayfish in Sweden, addressing both model uncertainty and method reliability, and 3) to use the model to predict the success of signal crayfish establishments over a larger area of Sweden.

One conclusion in Paper I was that modelling transition time instead of the transition probability has several advantages. Probabilistic models of transition time were uncommon and there was no example of any implementation for the establishment success using data on a single species. This motivated me to specify a probabilistic model of the time to establishment success of an introduced population.

To this end, I used information on the time of introduction and establishment for the first years of introductions of the American signal crayfish *Pacifastacus leniusculus* into Sweden. The signal crayfish is a non-indigenous species with a long invasion history and provides a best-case situation when it comes to data availability in risk analysis of biological invasions. Despite being one of the best datasets available for introductions of signal crayfish in Sweden, it had several characteristics typical for this kind of observational data that demand special attention.

First, the data was censored, i.e. for some populations the time of first introduction or the time of successful establishment was unknown. This required a time-to-event model of establishment success that can make use of information in censored data. My choice therefore fell on the accelerated failure time model, a regression-based model on the rate of establishment success with the capability of handling censored data (Kalbfleisch and Prentice 1981). The time-to-event models on establishment success that I found in published literature were either not fully probabilistic (Drake *et al.* 2005) or did not include the effect of covariates (Caley *et al.* 2008). I approached the uncertainty in the specification of the time-to-event model with an information-theoretical approach (Burnham and Anderson 2002). This approach uses the information of a model, given by its likelihood and the number of parameters, to assign relative weights on a number of alternative models based on empirical data. A good model has strong support from the observed data without using too many parameters. The use of the information-theoretical approach requires a probabilistic model for which the likelihood can be estimated from the data available. I therefore began specifying different candidate models for the failure rate over time (also known as the hazard function) and selected the best models based on the information-theoretical approach.

Second, the data showed severe multi-collinearity, i.e. strong correlations between covariates made it difficult to identify their separate (independent) effects on the response variable (Quinn and Keough 2002). I used two methods to derive the separate effects of covariates: model averaging (Burnham and Anderson 2002) and hierarchical partitioning (Chevan and Sutherland 1991). Model averaging is an information-theoretical method to estimate the effect of a covariate seen over several models making use of their relative weights, given by the likelihood and the number of parameters. Hierarchical partitioning is a method to estimate the independent effect of a covariate from all comparisons of the goodness of fit for all models with and without the covariate in question.

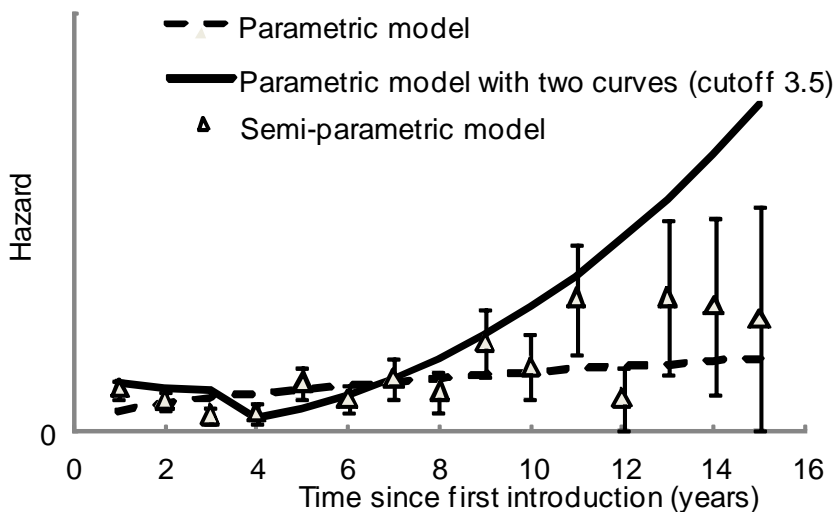


Figure 4. Curves showing the hazard of a crayfish population to succeed in establishing as a function of time since first introduction. I have used three different models: a parametric model with either increasing or decreasing hazard function, a parametric model being a combination of two hazard functions the first between 0 and 3.5 years after introduction and the second thereafter, and a semi-parametric model with no specific functional form of the hazard function.

The strongest support was found for a time-to-event model with a decaying and then increasing rate of establishment success over time (also known as the hazard function; Figure 4). Because the shape of the hazard function became more uncertain further away from the time of first introduction, we regarded predictions from the model within ten years after the first introduction as reliable. The probabilistic model predicted establishment success to be less than 50% within five years after first introduction over the current distributional range of signal crayfish in Sweden (Fig 8 in Paper II).

Among covariates related to air temperature, occurrence of fish species, and physical properties of the habitat, the length of the growing season constituted the most important and consistent predictor of establishment success. Based on our results, the establishment success of signal crayfish is expected to increase with the number of days when growth is possible, and decrease with the number of days with extremely high temperatures, which can be assumed to approximate conditions of stress (Jonsson and Edsman 1998, Verhoef and Austin 1999).

4.4 What uncertainty to expect in the distribution of an invading population

Given the assumption that the impact of a non-indigenous species is proportional to the range it occupies (Parker *et al.* 1999), the rate of increase in the loss (or gain) caused by the species can be approximated by its speed of range expansion (Neubert and Parker 2004) or the time it takes for the species to reach a certain range or destination (Smith *et al.* 2002). These parameters are strongly determined by the existence of extreme events such as long-distance dispersal (Higgins *et al.* 2003a) or the failure of populations to continue range expansion (Higgins *et al.* 2003b). Current spread models such as reaction-diffusion models or integro-difference equations can handle stochastic dispersal events, and range expansion is most often modelled as the expected range given a probabilistic model of the dispersal event (Kot *et al.* 1996, Neubert and Parker 2004). Because the time horizon of an ecological forecast is generally short (less than 50 years; Clark *et al.* 2001), we also need to look at the expected uncertainty in range expansion seen over a small number of dispersal events. In Paper III, I addressed this issue by performing explicit simulations of range expansion in artificial landscapes.

A landscape can be seen as consisting of patches, more or less suitable for survival and population growth. The amount and fragmentation of suitable habitat represent well-established descriptors of the spatial characteristics of a landscape (Fahrig 1997) and have been found to influence both dispersal success (With and King 1999, King and With 2002) and speed of range expansion (Shigesada *et al.* 1986, Turchin 1998). However, although data on landscape heterogeneity are readily available for probabilistic risk analysis, few attempts have been made to study how spatial characteristics of the landscape affect the uncertainty in range expansion (e.g. Minor *et al.* 2008). I approached this question in Paper III by deriving the expected probabilistic model of the endpoint speed of range expansion for two types of dispersal behaviour (passive and active), for different amounts of habitat and levels of habitat fragmentation, and for different time spans (measured as the number of dispersal events). I particularly asked 1) when information on dispersal behaviour and landscape structure was important for the uncertainty in range expansion, and 2) how the risk that a species becomes invasive changes when expanding into a landscape of a different spatial heterogeneity. The existence of extreme events was modelled by using extreme value theory to analyze the uncertainty in speed of range expansion.

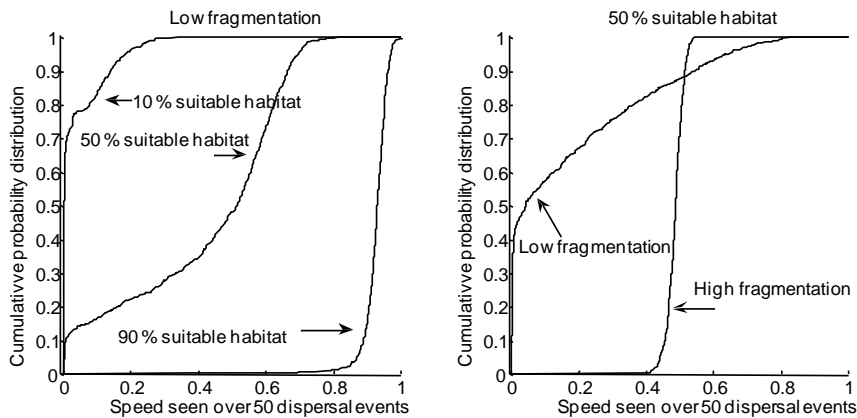


Figure 5. The risk of an expanding population to be invasive is always higher in a landscape with more suitable habitat (left), but can be both higher or lower in more fragmented landscape (right), everything else equal. When one cumulative probability distribution always is lower than another, stochastic dominance tells us that the risk of invasive spread will always be higher as well. A step curve is found when the distribution of possible values on speed has a small variation, whereas the opposite is a sign of large variation and possible extremes in range expansion.

I found that the overall risk of invasion, manifested by the cumulative probability function of range expansion, followed the amount of suitable habitat in the landscape, whereas the uncertainty in risk, manifested by the shape of the cumulative probability function, was dominated by the degree of fragmentation (Figure 5). Active dispersal behaviour in a landscape consisting of large unsuitable patches generated an expected uncertainty in range expansion. The magnitude of this uncertainty was strongly influenced by extreme events such as unusually fast advances of the expanded range (owing to long-distance dispersal) or populations being permanently stopped in their range expansion. The influence of extreme events on the uncertainty in speed of range expansion became smaller with time. For example, there was marked difference in what uncertainty to expect in expanded range seen over five compared to fifty dispersal events, especially for a population spreading with active dispersal (Figure 6).

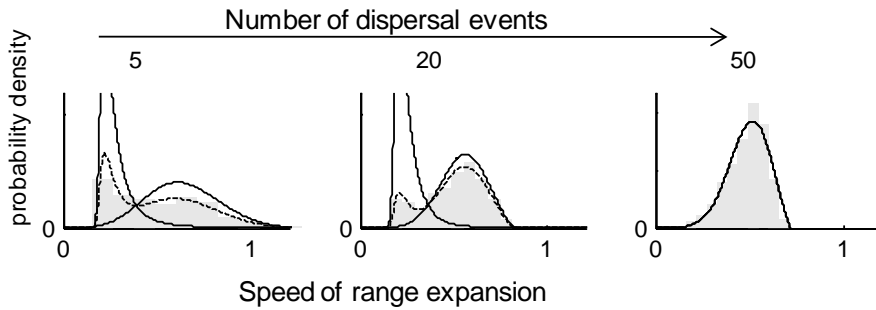


Figure 6. The results after characterizing uncertainty in the speed of range expansion of a spreading population seen over different number of dispersal events (the time horizon of the prediction). Seen over five dispersal events we should expect a large variation in speed and a probabilistic model of speed consist of a mix of two distributions, representing slow and normal spread. Enlarging the time horizon the probabilistic model appears as a single statistical distribution. Based on simulated values (histogram with gray bars) a mix of one or two Weibull distributions were fitted (solid lines) resulting in the probabilistic model (dashed line).

4.5 The value of species traits as predictors of invasion success

Information on species-specific traits may be useful when predicting the invasiveness of non-indigenous species. Considering the vast number of potentially invasive species, the total costs for collecting information on species traits and then performing the necessary risk analyses are expected to be high. One way to use limited societal resources efficiently is to subject the screening models to cost-benefit analyses, weighting the costs of doing risk analysis against the potential reduction in future expected losses caused by the invasive species (if introduced).

In Paper IV I performed a pre-posterior value of information analysis to evaluate the benefit of a predictive model and then used the model in a specific case-study to ask if particular species should be stopped or allowed to spread in a particular area. A value-of-information analysis evaluates a predictive model in a Bayesian decision context. The analysis is said to be pre-posterior because the value of information is being evaluated before the information is collected.

The probabilistic model in Paper IV predicts the invasiveness of species based on information on both species-specific traits and the base-rate of invasiveness, i.e. the proportion of invasive species among those introduced. The base-rate of invasiveness influences both the ability to provide accurate predictions and the expected losses of societal resources to be considered by a decision maker. In this regard, it is also necessary to consider the uncertainty in the base-rate. One objective in Paper IV was therefore to determine whether uncertainty in the base-rate of invasiveness influences 1) the benefit of using species-specific information to screen for invasive species, and 2) the benefit of increasing the accuracy of the predictive model.

A more accurate model was always more beneficial to a decision maker, and the uncertainty in the base-rate significantly affected the benefit of the predictive model. Thus, it is important to account for uncertainty in the base-rate of invasiveness when evaluating the benefit of models used to predict invasiveness of non-indigenous species. However, counter-intuitively, the benefit of the model was not necessarily higher under reduced uncertainty in the base-rate value.

The pre-posterior value of information analysis was implemented in a case study with the purpose of deriving the benefit of using species-specific traits when screening for potentially invasive macroalgae in Europe (Nyberg and Wallentinus 2005). The benefit of a predictive model based on species traits of invasive and non-invasive macroalgae was estimated to be at most 20% of the loss of resources resulting from the introduction of one invasive species. According to a recent European assessment (Kettunen *et al.* 2008), this figure corresponds to a net present value of 3.4 million euro per species and year.

When working with paper IV, I came to realize that predictive models of invasiveness translate current knowledge, such as expert's know-how and empirical data, into information supporting decision making. Therefore, it became natural to think of the model itself as information and to ask how this factor affected the accuracy and benefit of the predictive model used in this paper. Both the accuracy of predictions and the benefit of the model based on species traits increased with the amount of information contained in the model, evaluated with the likelihood function penalizing for model complexity, i.e. the Akaike information criteria (AIC) (Figure 7).

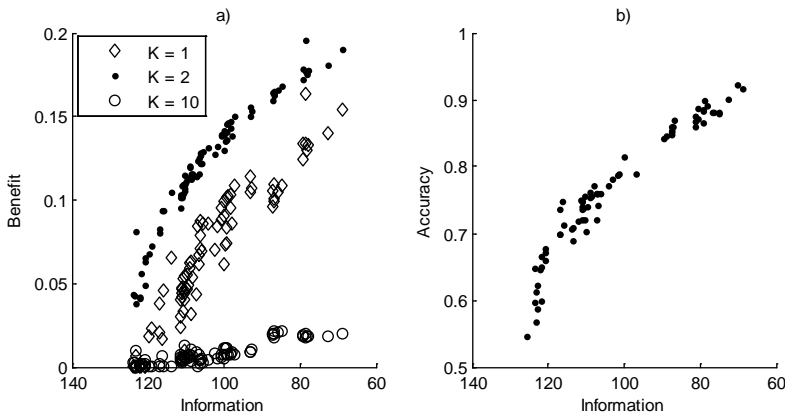


Figure 7. The relationship between the information contained in the model used to predict invasiveness of macroalgae (measured as the Akaike information criteria (Burnham and Andersson 2002)) and a) model benefit (measured as the value of information), and b) model accuracy (measured as the area under the ROC-curve (Fielding and Bell 1997)). Benefit is derived for three different ratios of the cost associated with an invasive species compared to the cost associated with stopping a non-invasive species from being introduced ($K = 1, 2$ and 10).

4.6 Robust prevention and control of an invaded system

The biological invasion endpoint that is most relevant from a societal perspective lies in the end of the invasion chain in the impact from an invasive species on the invaded system (Keith Hayes personal communication). Because the effects from biological invasions may be irreversible and established populations difficult to eradicate, measures to manage invasions should be directed towards the early phase of invasions. The recommended strategy of prevention is to stop potentially invasive species from being introduced in combination with monitoring for early detection followed by rapid measures for control of introduced species (McNeely *et al.* 2001, Lodge *et al.* 2006). Successful management of biological invasions depends on finding optimal strategies for how to allocate resources between prevention and control of introduced non-indigenous species. Prevention is costly and the immediate gain more difficult to grasp compared to controlling species in the system, especially after seeing the consequences they have on the economic, environmental or human health.

The uncertainty in predictions of the outcome of a single species introduction increases as we move along the invasion chain. By adopting a system perspective on the problem (Haines 2009) some of these uncertainties can be circumvented by focusing on the progress of the performance of an invaded system over time instead of the states of single species invasions (Figure 2). A recognized indicator of the state of ecological systems with respect to invasions is the number of species with an undesired impact (McGeoch *et al.* 2006, Molnar *et al.* 2008), and not the total number of non-indigenous species. In my last study I therefore specified a state dynamic model of the number of established non-indigenous species in a system over time. By regarding successful species establishments as a stochastic process, initiating events causing risk occurred with certain intensity. Our knowledge on establishments processes and possible dynamics are limited, and the optimal strategy should therefore also be robust to epistemic uncertainty (Box 3).

The objective in Paper V was to find a robust allocation between prevention and control of multi-species invasions into a system. I addressed this question by designing an analysis that 1) was based on available data on impact of biological invasions, 2) adopted a system perspective on risk, and 3) considered epistemic uncertainty of the invasion process.

Between 1900 and 1990, every second or third year a new non-indigenous species have established into the Baltic Sea. During this period, non-indigenous species have been introduced more often, but since most species fail to establish, we do not know the exact number. By focusing on the performance of the system, measured as the number of established species, the uncertainty in numbers become smaller.

We found that resources allocated to control should be the same for different values of the quantified uncertainty in intensity and its dynamics for the Baltic Sea. We therefore conclude that the strategy to allocate resources to control until the maximum eradication success is maintained is robust to epistemic uncertainty in intensity and its dynamics. This calls for an improvement of eradication success. Resources to be allocated to prevention were sensitive to the assumption on the prevailing type of system dynamics. Resources allocated to prevention was not robust to epistemic uncertainty in dynamics, but were robust to epistemic uncertainty in intensity for a given type of dynamics. This means that the allocation of resources to prevention derived from the suboptimal solution under full uncertainty is to prefer. This result demonstrates that more research is needed to increase our understanding of the dynamics of establishment processes.

4.7 Summary of my research contributions

My research contributions have been the quantification of uncertainty in some biological invasion endpoints, using empirical (Paper II, IV and V) and artificial data (Paper III).

I have also suggested solutions to problems related to predicting under uncertainty. I have produced an overview to probabilistic models of establishment success (Paper I). I have shown that it is possible to implement a model for time-to-event analysis common for other applications on risk analysis on ecological problems where prediction is an important issue (Paper II). I have shown how extreme value theory can be used to answer questions on the uncertainty in a biological invasion endpoint (Paper III). I have proposed a way to implement pre-posterior Bayesian value of information analysis to evaluate probabilistic models (Paper IV). I have specified a probabilistic model for the risk posed by biological invasions that is both easy to implement using already available data on invasions and that address the large uncertainty in risk by using a system perspective (Paper V).

Finally, my research contribution has been to implement issues of uncertainty into scientific questions. Uncertainty is implemented in two directions. One direction is to ask for the characteristics of uncertainty given certain type of knowledge. This was done in Paper III where I ask how ecological variables influence the uncertainty in an endpoint and thereby the risk. The other direction is to explore the sensitivity to uncertainty. This was done when I asked for the effect of uncertainty in an endpoint on the value of predicting (Paper IV) or the robustness in decision making (Paper V).

5 GENERAL DISCUSSIONS

The general aim of this thesis is to shed light on what it means to predict future events in ecology, with special emphasis on biological invasions. Predicting the outcome of biological invasions must often be done before the first time a particular species is introduced into a particular system, i.e. before any historical data on the endpoint for risk analysis is available. Such predictions are inherently difficult to make, given the argument that “probability density function cannot be constructed for one-time events with no precedents” (Horan *et al.* 2002 citing Williamson 1996). The aim of probabilistic risk analysis is to quantify uncertainties related to the undesired event, for example, a successful invasion. The methods used in probabilistic risk analysis are useful for predicting futures in ecology – the only difference being that the word risk is not needed.

A number of factors must be considered when using probabilistic analysis to predict with uncertainty. First, it is necessary to state the purpose of predicting. In the same way as risk analysis has no value in itself and is undertaken with the specific purpose of making decisions (Aven 2003), predictions of future ecology are done with a specific purpose. The purpose of predictions and the characteristics of the user are important for how predictions are made. Second, although the availability of empirical data remains a critical issue, predictions can be made at several different levels, depending on to what extent the background information includes historical data, expert judgement or modelling (Apeland *et al.* 2002). A probabilistic analysis should be regarded as conditional on the background information (Aven 2010) and a unifying framework to predict futures should be able to deal with different strengths and types of background information. Finally, it is necessary to consider the role of subjectivity when predictions have to be made with no or little data, or when the interpretation of data is affected by expert’s know-how and risk perception (Burgman 2000) and world view (Brown 2001). Predictions are more-or-less based on subjective knowledge which, if not devoted proper consideration, may reduce the trust in predictions. A unifying framework to predict ecological futures should therefore suggest how to interpret uncertainty under different types of quantification.

In Paper I the Bayesian approach to predicting were taken as an example of a good treatment of uncertainty due to its capability of handling both objective and subjective quantification of probabilities. I am aware that this statement is naive; the Bayesian approach has been shown to be difficult to implement in practise. I do not argue for the Bayesian approach, however

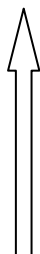
its ability to make inference under conditions of sparse data (Dennis 1996) and the logic in Bayesian models (Clark 2005) makes it worthwhile and perhaps necessary to consider for probabilistic analysis.

5.1 The interpretation of probabilistic output for different strengths of background information

In Paper I the probabilistic predictions of establishment success found in the literature could be categorised as likelihood-based or of the forecasting type. Let me discuss the origin of these two types of predictions and their interpretation. In my view, both of these types of prediction can be interpreted under the unifying framework for risk analysis suggested by Aven (2010) (also described in Apeland *et al.* 2002, Aven and Kvaloy 2002, Aven and Kristensen 2005). In this approach, the focus is on observable quantities describing the state of the world; let us denote it by Y . More precisely, Y is a "quantity expressing a state of the world that is unknown at the time of the analysis but will, if the system being analyzed is actually implemented, take some value in the future, and possibly become known" (Aven 2003). They also suggest that the end product of a probabilistic (risk) analysis to be the predictive uncertainty distribution of Y . The interpretations of probabilistic output are then different dependent on the strength of background information (Table 2).

First, let us consider the case when data exist on historical events on Y . In this case, the predictive distribution $P(Y \leq y)$ (where P stands for probability) can be empiric, estimated directly from data with no particular statistical model in mind, or parametric as a probability model, $P(Y \leq y | \lambda)$, with (for simplicity) the parameter λ . In the latter case, the prediction is likelihood-based (cf. Paper I), and the end product of the probabilistic analysis is either point estimates of parameter values in the underlying statistical model, estimated with the classical frequentist approach, or the updated posterior distribution of the parameters based on the likelihood, when using the Bayesian approach. In Paper II, the maximum likelihood estimates of parameters in the probability model were used to predict the predictive posterior of the time to successful establishment. Since we have observed Y , there exists an underlying statistical population for Y , and therefore the parameters governing the uncertainty in this population, such as the mean and variance, are in themselves random variables. When the uncertainty in the parameters for these random variables may be valuable for prediction, the posterior distribution of parameters is an end product of the probabilistic analysis.

Table 2. The interpretation of probabilistic output for various strengths of background information determined by the type of available data. See the text for details.

Strength of background information	Available empirical data	Notations	Quantified uncertainty	Comment
	Data	Y	Predictive posterior and posterior	Likelihood-based prediction
	Data on another variable and a model	X and $g(.)$	Predictive posterior	Forecasting-type of prediction
	Data on similar variables	Z	Subjective predictive posterior	Difficult interpretation!
	No data		Subjective posterior	Confidence interpretation

Now consider the case when no data is available on Y , and data are available on quantities regarded as “similar” to Y , let us denote them by Z . What is regarded as a “similar” is judged by the analyst. It could be species introduced into the same region and from the same taxonomic group. Species are made more similar in a statistical meaning by for example correcting for phylogenetic control (Fisher and Owens 2004). Observations are made more similar by correcting for covariates, for example, using a generalized linear model. The uncertainty in Y can then be quantified the same way as in the previous examples replacing Y by Z . However, the probabilistic output is given a slightly different interpretation. Since the values in Z are observations from other populations than a hypothetical underlying population of Y , the parameter λ is no longer an observable quantity and the posterior is not an end product of the prediction. The predictive posterior $P(Y \leq y)$ quantified as $P(Z \leq z)$ can simply be interpreted as our subjective uncertainty distribution. Another approach is to regard the values in Z as part of the background information and argue for a probability distribution for each z in Z , using Bayesian approach assigning uninformative priors to derive the posterior distribution for Z (see Aven and Kvaloy 2002). In this latter case, the quantified uncertainty in Y has a more rigorous motivation than in the previous case.

When no data is available on Y , another alternative is to use data on a lower level of detail, denoted by X . The available knowledge between X and Y are then reflected in a deterministic model, $y = g(x)$. Examples of this type of forecasting-type of predictions (cf. Paper I) are population viability analysis (Beissinger and McCullough 2002) or establishment success (Drake *et al.* 2006). In these cases $g(\cdot)$ is a population dynamic model based on estimated life history parameters. The predictive distribution for Y may then be

$$P(Y \leq y) = \int_{\{x: g(x) \leq y\}} dP(X \leq x).$$

The predictive distribution of Y can be derived by Monte Carlo simulations given an empiric or parametric probability distribution of X . It can alternatively be assessed as the predictive posterior in a Bayesian analysis

$$P(Y \leq y) = E[P(Y \leq y | \lambda)] = \int_{\lambda} \int_{\{x: g(x) \leq y\}} dP(X \leq x | \lambda) dH(\lambda),$$

where $P(X \leq x | \lambda)$ is a probability model for the uncertainty in X given the parameter λ , and $H(\lambda)$ is an uncertainty distribution of the parameter λ . Following the probability of frequency or the combined classical and Bayesian approaches, the interpretation of $P(X \leq x | \lambda)$ in Paper V was a model of stochastic uncertainty given the parameter λ , and $H(\lambda)$ an expression of the epistemic uncertainty in the parameter λ (Apeland *et al.* 2002).

A model is a simplifying description of the world. No model is true and several possible models could be used to predict Y , let us call them g_1 , g_2 , etc, which are part of the background information. The approach is then to weight each model according to our confidence in the models ability to accurately predict Y , as $P(Y \leq y) = P(Y \leq y | g_1) \cdot w_1 + P(Y \leq y | g_2) \cdot w_2 + \text{etc}$ (Aven 2010). In Paper II, I weighted models in this way using weights derived from the likelihood and an information theoretic approach (Burnham and Anderson 2002).

In our last case, no relevant data exists to predict Y . We can proceed as above, but the interpretation is different. The so called confidence interpretation is to view $P(Y \leq y | \lambda)$ as a candidate for our subjective probability that $Y \leq y$ given that λ is chosen and $H(\lambda)$ as a measure of our confidence in these predictions. When no data exists $P(Y \leq y | \lambda)$ is a model of our subjective belief and does not describe the world, and $H(\lambda)$ is no longer a measure of uncertainty (Apeland *et al.* 2002).

In any of these cases, focus is on observable quantities and their uncertainty, probability is used as a measure of uncertainty of the true value

of observables, and the predictive posterior is conditional on the background information (Aven 2010). Besides the extent of available data, the strength on background information depends on the suitability and accuracy of models that can be used for prediction. Good probabilistic models evaluated with empirical data provides the type of information needed to make transparent and scientifically based predictions, and I discuss how below.

5.2 From data to information through the eyes of a probabilistic model

Information has been defined as “data that has been processed into a form that is meaningful to the recipient and is of real or perceived value in current or prospective actions or decisions” (March and Smith 1995). In order to have information we need constructs that organize our thoughts about an issue such that we can compile our knowledge into predictions of future events. One such construct is the likelihood.

In this thesis, the term likelihood was first used in the CBD definition on risk analysis of biological invasions which had the “aim to assess the likelihood of establishment success and the consequences” (CBD 2010). A qualitative interpretation of likelihood is a statement of how likely something is to occur, for example, less likely or very likely. A quantitatively interpretation of likelihood is the probability that something will occur. A mathematical or technical definition of likelihood is the joint-probability density of a model given data. The joint-probability, $f(\text{data} \mid \text{model})$, is a quantification of the uncertainty in the events to be predicted. The likelihood, $L(\text{model} \mid \text{data})$, express how probable this model is in relation to other models. In information theory the likelihood is interpreted as a measure of information. Models containing more information are more accurate and have higher benefit in decision making (Paper IV).

The likelihood is important in Bayesian inference, where – according to the likelihood principle - data is only allowed to enter through the likelihood function. The likelihood is used in classical inference, such as when parameters are estimated by maximizing the likelihood function and the use of likelihood ratio tests. Information theoretic approaches to inference, such as model selection and model averaging, use the likelihood as a measure of information (Burnham and Anderson 2002). In my view both information theoretic and Bayesian approaches are useful in predicting. Since the information theoretic approach only works when data is available, its usefulness is to describe and explain the world, for example, by finding important and robust predictors of future events and evaluating

proper parametric probabilistic models given the available sources of background information. In addition, the Bayesian approach (and its decedents) is able to combine several types of quantifications of uncertainty. So, why not only use the Bayesian approach? With the purpose of describing and explaining the world, the classical frequentist approach to statistics has proved to be successful (Dennis 1996) while the Bayesian models easily become unnecessary complicated (Clark 2005). An alternative could be to use a (well motivated) less strict Bayesian approach (e.g. Apeland *et al.* 2002, Aven and Kvaloy 2002).

Once we have a probabilistic model, we obtain information by the likelihood. The task is then to arrive at a good probabilistic model for an endpoint at a specific resolution and for a certain type of information. A good probabilistic model should capture the nature of the uncertainty in data such as encompass both variability and uncertainty arising from the way data is sampled (Paper II). What uncertainty to expect in a given biological invasion endpoint conditioned on a specific type of information on the system (Paper III). How to enter important covariates in a probabilistic model is not straightforward. Propagule pressure, for example, is an important predictor of establishment success (Lockwood *et al.* 2005) that is entered as a covariate in a statistical model or by the specification of a parametric establishment curve in a state dynamic model (cf. Paper I).

5.3 From information to decision ... and back again

According to the Bayesian approach, the decision maker is to choose the decision alternative that minimizes expected loss, given by the predictive posterior distribution of the loss. In Paper IV and V I let the decision maker minimize expected loss assuming risk neutrality. The Bayesian (expected utility) approach is a normative decision theory showing how rational decision ought to be done, but may not capture how decisions are done in the real world. In Paper IV I used the expected utility approach to quantify the benefit of a predictive model and the decision rule was an instrument of the benefit analysis. Paper V was more focused on realistic decision making, but I used the expected utility approach as a starting point. Using an expected utility strategy is risky since uncertainties in utilities and probabilities are not visible in the end product (Burgman 2005). Variations of the Bayesian approach have tried to distinguish between risk and uncertainty (de Rocquigny *et al.* 2008). Decision making under uncertainty involve a trade-off between robustness to uncertainty and the performance of the decision strategy (Regan *et al.* 2005a, Clark *et al.* 2001). I suspect the influence of uncertainty on the benefit of a model (Paper IV) or the optimal

strategy (Paper V) would have been larger if aversion to risk and/or aversion to uncertainty had been taken into account.

Under large uncertainty the focus changes from predicting effect to vulnerability (Shrader-Frechette 1991). The shift is then from prediction single events in a biological invasions to the performance of an invaded system (Catford *et al.* 2009, Paper V). Another reason to predict system performance is that decision making are directed towards handling several threats initiated over time, acknowledging the complexity of systems. When predicting with a system perspective (Figure 1) time is important, because timing of the growing of populations, the extinction of species, the ongoing range expansion, the payoff from management actions, new threats, temporal variation and perhaps evolutionary adaptation is what determines the performance of the system. Adopting a system perspective on risk (and what is to be predicted), the risk triplet questions What can go wrong?, How likely is it? and What are the consequences?, are expanded with a fourth question

Over what time frame?

(Haimes 2009). Probabilistic models of time instead of the probability of single events should receive more attention, especially if it means that we can get more information out of data (Paper II). Predicting using a system perspective requires probabilistic models of endpoint events measured as a transition time as opposed to transition probability (Paper I).

The needs and behaviour of the decision maker determine what to predict and how to predict. The communicating with decision makers therefore start in the direction from the decision maker to the analyst. Communication in the other direction should strive to present the output from probabilistic analysis so that decision makers understand and use them. A presentation of a probabilistic output is the probability of making different types of errors. There are probabilistic models that have the error distribution as their only output (Paper I), i.e. the probabilistic model is incorporated in a decision model.

6 FINAL REMARKS

Three reasons to predict futures in ecology are to preserve biodiversity, protect biosecurity and reduce negative impact from climate change. Three reasons not to predict futures in ecology are large uncertainties, the occasional lack of empirical data and the intrusion of subjective judgements into the analyses. Approaching risk and uncertainty means “to reflect our knowledge and lack of knowledge about the world” (Aven and Kristensen 2005). Knowledge based (epistemic) uncertainty should not be regarded as high or low, but as more or less manageable, and one could argue that it is a responsibility of scientists to make uncertainty manageable (Knaggård 2009). Methods of probabilistic risk analysis open up for a transparent and rigorous treatment of uncertainty as a basis for scientifically based decisions.

This thesis is about probabilistic analysis. Alternative approaches to predicting the outcome of invasions under uncertainty are based on, for example, measures of similarity between sites (Herborg *et al.* 2007) or species communities (Gevrey *et al.* 2006). An argument against predictions based on similarities is that uncertainty remains unquantified. The error in this argument is that when looking at how decisions are actually made. People tend to base their decisions on previously known cases rather than maximizing the expected utility as in probabilistic analyses. Alternative decision theories, such as bounded rationality (in Burgman 2005) and case-based decision theory (Gilboa and Schmeidler 1995), consider the outcome of decisions or events in previous and similar cases. This stresses the importance of sharing data and information on past actions, as emphasized in evidence-based policy-making (Pulling and Knight 2009).

The most valuable source of information to probabilistic analysis is the knowledge of the world hidden in empirical data. To predict (or doing a risk analysis) is not a scientific task, in contrast to the production of background information and the development of methodologies for probabilistic analysis. However, uncertainty needs to be incorporated into the scientific part of the prediction process. This may require training in, for example, Bayesian methods and how to communicate uncertainties (Kinzig *et al.* 2003). When it comes to biological invasions, some ecologists claim that while describing invasions is relatively easy, explaining is much harder and predicting often extremely difficult (Williamson 2006). Whereas describing is necessary for providing relevant data and explaining is necessary for producing good predictive models, is it necessary to challenge the scientific value of ecological predictions.

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REFERENCES

- Akcakaya, H. R., S. Ferson, M. A. Burgman, D. A. Keith, G. M. Mace, and C. R. Todd. 2000. Making Consistent IUCN Classifications under Uncertainty. *Conservation Biology* **14**:1001-1013.
- Andersen, M. C., H. Adams, B. Hope, and M. Powell. 2004. Risk assessment for invasive species. *Risk Analysis* **24**:787-793.
- Apeland, S., T. Aven, and T. Nilsen. 2002. Quantifying uncertainty under a predictive, epistemic approach to risk analysis. *Reliability Engineering & System Safety* **75**:93-102.
- Aven, T. 2003. Foundations of risk analysis. John Wiley & Sons Ltd., New York, NY.
- Aven, T. 2010. Some reflections on uncertainty analysis and management. *Reliability Engineering & System Safety* **95**:195-201.
- Aven, T. and V. Kristensen. 2005. Perspectives on risk: review and discussion of the basis for establishing a unified and holistic approach. *Reliability Engineering & System Safety* **90**:1-14.
- Aven, T. and J. T. Kvaloy. 2002. Implementing the Bayesian paradigm in risk analysis. *Reliability Engineering & System Safety* **78**:195-201.
- Barry, S. C., K. R. Hayes, C. L. Hewitt, H. L. Behrens, E. Dragsund, and S. M. Bakke. 2008. Ballast water risk assessment: principles, processes, and methods. *Ices Journal of Marine Science* **65**:121-131.
- Bedford, T. and R. Cooke. 2001. Probabilistic risk analysis: foundations and methods. Cambridge University Press, Cambridge.
- Beissinger, S. R. and D. R. McCullough. 2002. Population viability analysis. *Population viability analysis*.:i-xvi, 1-577.
- Berglund, H. 2009. The treath from non indigenious species - ecosystem vulnerability, global distribution and co-occurences with other major threats, Doctoral thesis, Lund University, Lund.
- Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* **23**:453-460.

– learning by probabilistic risk analysis of biological invasions

- Brown, J. S. 2001. Ngongas and Ecology: On Having a Worldview. *Oikos* **94**:6-16.
- Burgman, M. A. 2000. Population viability analysis for bird conservation: Prediction, heuristics, monitoring and psychology. *Emu* **100**:347-353.
- Burgman, M. A. 2005. Risks and decisions for conservation and environmental management Cambridge University Press, Cambridge, UK.
- Burnham, K. P. and D. R. Anderson. 2002. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.
- Caley, P., R. H. Groves, and R. Barker. 2008. Estimating the invasion success of introduced plants. *Diversity and Distributions* **14**:196-203.
- Carlsson, F. and M. Kataria. 2008. Assessing management options for weed control with demanders and non-demanders in a choice experiment. *Land Economics* **84**:517-528.
- Carlton, J. T. and G. M. Ruiz. 2005. Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. *Invasive alien species: a new synthesis*:58.
- Catford, J. A., R. Jansson, and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* **15**:22-40.
- CBD (Convention of Biological Diversity). 2010. <http://www.cbd.int/> January 2010.
- Chapman, P. M. 2002. Integrating toxicology and ecology: Putting the "eco" into ecotoxicology. *Marine Pollution Bulletin* **44**:7-15.
- Chevan, A. and M. Sutherland. 1991. Hierarchical partitioning. *American Statistician* **45**:90-96.
- Clark, J. S. 2005. Why environmental scientists are becoming Bayesians. *Ecology Letters* **8**:2-14.
- Clark, J. S., S. R. Carpenter, M. Barber, S. Collins, A. Dobson, J. A. Foley, D. M. Lodge, M. Pascual, R. Pielke, Jr., W. Pizer, C. Pringle, W. V. Reid, K. A. Rose, O. Sala, W. H. Schlesinger, D. H. Wall, and D. Wear. 2001. Ecological forecasts: An emerging imperative. *Science* **293**:657-660.

- Colautti, R. I. and H. J. MacIsaac. 2004. A neutral terminology to define 'invasive' species. *Diversity and Distributions* **10**:135-141.
- Colyvan, M. 2008. Is probability the only coherent approach to uncertainty? *Risk Analysis* **28**:645-652.
- Cook, D. C. and R. W. Fraser. 2008. Trade and invasive species risk mitigation: Reconciling WTO compliance with maximising the gains from trade. *Food Policy* **33**:176-184.
- Coreau, A., G. Pinay, J. D. Thompson, P. O. Cheptou, and L. Mermet. 2009. The rise of research on futures in ecology: rebalancing scenarios and predictions. *Ecology Letters* **12**:1277-1286.
- Cox, R. T. 1946. Probability, frequency and reasonable expectation. *American Journal of Physics* **14**:1-13.
- de Rocquigny, E., N. Devictor, and S. Tarantola, editors. 2008. *Uncertainty in industrial practice - a guide to quantitative uncertainty management*. Wiley.
- Dennis, B. 1996. Discussion: Should ecologists become Bayesians? *Ecological Applications* **6**:1095-1103.
- Drake, J. M., K. L. S. Drury, D. M. Lodge, A. Blukacz, N. D. Yan, and G. Dwyer. 2006. Demographic stochasticity, environmental variability, and windows of invasion risk for *Bythotrephes longimanus* in North America. *Biological Invasions* **8**:843-861.
- Drake, J. M. and D. M. Lodge. 2004. Global hot spots of biological invasions: evaluating options for ballast-water management. *Proceedings of the Royal Society Biological Sciences Series B* **271**:575-580.
- EEA (European Environment Agency). 2004. *European environmental indicators*. EEA.
Available from <http://themes.eea.europa.eu/indicators/> (accessed January 2010). Copenhagen.
- Ellison, A. M. 1996. An introduction to Bayesian inference for ecological research and environmental decision-making. *Ecological Applications* **6**:1036-1046.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* **61**:603-610.
- Falk-Petersen, J., T. Bohn, and O. T. Sandlund. 2006. On the numerous concepts in invasion biology. *Biological Invasions* **8**:1409-1424.

- Fielding, A. H. and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**:38-49.
- Fisher, D. O. and I. P. F. Owens. 2004. The comparative method in conservation biology. *Trends in Ecology & Evolution* **19**:391-398.
- Gevrey, M., S. Worner, N. Kasabov, J. Pitt, and J.-L. Giraudel. 2006. Estimating risk of events using SOM models: A case study on invasive species establishment. *Ecological Modelling* **197**:361-372.
- Gilboa, I. and D. Schmeidler. 1995. Case-Based Decision Theory. *The Quarterly Journal of Economics* **110**:605-639.
- Gozlan, R. E. and A. C. Newton. 2009. Biological Invasions: Benefits versus Risks. *Science* **324**:1015-1015.
- Gren, I. M., L. Isacs, and M. Carlsson. 2009. Costs of Alien Invasive Species in Sweden. *Ambio* **38**:135-140.
- Gärdenfors, P. and N. E. Sahlin. 1982. Unreliable probabilities, risk-taking, and decision-making. *Synthese* **53**:361-386.
- Haimes, Y. Y. 2009. On the Complex Definition of Risk: A Systems-Based Approach. *Risk Analysis* **29**:1647-1654.
- Halpern, B. S., H. M. Regan, H. P. Possingham, and N. M. A. McCarthy. 2006. Rejoinder: Uncertainty and decision making. *Ecology Letters* **9**:13-14.
- Hansson, S. O. 1999. A philosophical perspective on risk. *Ambio* **28**:539-542.
- Hayes, K. R. 1997. A review of ecological risk assessment methodologies. CHRIMP technical report.
- Hayes, K. R. and S. C. Barry. 2008. Are there any consistent predictors of invasion success? *Biological Invasions* **10**:483-506.
- Heger, T. and L. Trepl. 2003. Predicting biological invasions. *Biological Invasions* **5**:313-321.
- Helton, J. C. and W. L. Oberkampf. 2004. Alternative representations of epistemic uncertainty. *Reliability Engineering and System Safety* **85**:1-10.

- Herborg, L.-M., C. L. Jerde, D. M. Lodge, G. M. Ruiz, and H. J. MacIsaac. 2007. Predicting invasion risk using measures of introduction effort and environmental niche models. *Ecological Applications* **17**:663-674.
- Higgins, S. I., J. S. Clark, R. Nathan, T. Hovestadt, F. Schurr, J. M. V. Fragoso, M. R. Aguiar, E. Ribbens, and S. Lavorel. 2003a. Forecasting plant migration rates: Managing uncertainty for risk assessment. *Journal of Ecology* **91**:341-347.
- Higgins, S. I., S. Lavorel, and E. Revilla. 2003b. Estimating plant migration rates under habitat loss and fragmentation. *Oikos* **101**:354-366.
- Horan, R. D., C. Perrings, F. Lupi, and E. H. Bulte. 2002. Principal Paper Sessions The Economics of Invasive Species Management: Biological Pollution Prevention Strategies under Ignorance: The Case of Invasive Species. *American Journal of Agricultural Economics* **84**:1303-1310.
- Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* **46**:10-18.
- Hulme, P. E., P. Pysek, W. Nentwig, and M. Vila. 2009. ECOLOGY: Will Threat of Biological Invasions Unite the European Union? *Science* **324**:40-41.
- IPCC. 2007a. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.*in* M. L. C. Parry, O F. Palutikof, J P. van der Linden, P J. Hanson, C E. , editor. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- IPCC. 2007b. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.*in* R. K. Pachauri and A. Reisinger, editors., Geneva, Switzerland
- Johnson, J. B. and K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology & Evolution* **19**:101-108.
- Jonsson, A. and L. Edsman. 1998. Moulting strategies in freshwater crayfish *Pacifastacus leniusculus*. *Nord. J. Freshw. Res.* **74**:141–147.
- Kalbfleisch, J. D. and R. L. Prentice. 1981. The statistical analysis of failure time data. Wiley.

- Kaplan, S. and B. J. Garrick. 1981. On The Quantitative Definition of Risk. *Risk Analysis* **1**:11-27.
- Keller, R. P., K. Frang, and D. M. Lodge. 2007. Preventing the spread of invasive species: Economic benefits of intervention guided by ecological predictions. *Conservation Biology* **22**:80-88.
- Kettunen, M., P. Genovesi, S. Gollasch, S. Pagad, U. Starfinger, P. ten Brink, and C. Shine. 2008. Technical support to EU strategy on invasive species (IS) - Assessment of the impacts of IS in Europe and the EU (Final module report for the European Commission). Institute for European Environmental Policy (IEEP), Brussels, Belgium. 40 pp. + Annexes, May 2008, (DG ENV contract).
- King, A. W. and K. A. With. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecological Modelling* **147**:23-39.
- Kinzig, A. P., D. Starrett, K. Arrow, S. Aniyar, B. Bolin, P. Dasgupta, P. Ehrlich, C. Folke, M. Hanemann, G. Heal, M. Hoel, A. Jansson, B. O. Jansson, N. Kautsky, S. Levin, J. Lubchenco, K. G. Maler, S. W. Pacala, S. H. Schneider, D. Siniscalco, and B. Walker. 2003. Coping with uncertainty: A call for a new science-policy forum. *Ambio* **32**:330-335.
- Klinke, A. and O. Renn. 2002. A new approach to risk evaluation and management: Risk-based, precaution-based, and discourse-based strategies. *Risk Analysis* **22**:1071-1094.
- Knaggård, Å. 2009. Vetenskaplig osäkerhet i policyprocessen - en studie av svensk klimatpolitik (in swedish). Doctoral Thesis, Lund University, Lund.
- Kolar, C. S. and D. M. Lodge. 2001. Progress in invasion biology: Predicting invaders. *Trends in Ecology and Evolution* **16**:199-204.
- Kolar, C. S. and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in North America. *Science* **298**:1233-1236.
- Kolmogorov, A. N. 1956 (original version in russian from 1933). *Foundations of the Theory of Probability*. Chelsea Publishing Company, New York.
- Kot, M., M. A. Lewis, and P. Van Den Driessche. 1996. Dispersal data and the spread of invading organisms. *Ecology* **77**:2027-2042.

- Larson, B. M. H. 2007. Who's invading what? Systems thinking about invasive species. *Canadian Journal of Plant Science* **87**:993-999.
- Leprieur, F., S. Brosse, E. Garcia-Berthou, T. Oberdorff, J. D. Olden, and C. R. Townsend. 2009. Scientific uncertainty and the assessment of risks posed by non-native freshwater fishes. *Fish and Fisheries* **10**:88-97.
- Leung, B., D. M. Lodge, D. Finnoff, J. F. Shogren, M. A. Lewis, and G. Lamberti. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society of London Series B-Biological Sciences* **269**:2407-2413.
- Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* **20**:223-228.
- Lodge, D. M., S. Williams, H. J. MacIsaac, K. R. Hayes, B. Leung, S. Reichard, R. N. Mack, P. B. Moyle, M. Smith, D. A. Andow, J. T. Carlton, and A. McMichael. 2006. Biological invasions: Recommendations for US policy and management. *Ecological Applications* **16**:2035-2054.
- Ludwig, D. 1996. Uncertainty and the assessment of extinction probabilities. *Ecological Applications* **6**:1067-1076.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* **10**:689-710.
- March, S. T. and G. F. Smith. 1995. Design and natural-science research on information technology. *Decision Support Systems* **15**:251-266.
- McCarty, L. S. and M. Power. 2000. Approaches to developing risk management objectives: an analysis of international strategies. *Environmental Science and Policy* **3**:311-319.
- McGeoch, M. A., S. L. Chown, and J. M. Kalwij. 2006. A global indicator for biological invasion. *Conservation Biology* **20**:1635-1646.
- McNeely, J. A., H. A. Mooney, L. E. Neville, P. Schei, and J. K. Waage, editors. 2001. *A Global Strategy on Invasive Alien Species*, Gland Switzerland, and Cambridge, UK.
- Meyerson, L. A. and J. K. Reaser. 2003. Bioinvasions, bioterrorism, and biosecurity. *Frontiers in Ecology and the Environment* **1**:307-314.

- Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.
- Minor, E. S., R. I. McDonald, E. A. Treml, and D. L. Urban. 2008. Uncertainty in spatially explicit population models. *Biological Conservation* **141**:956-970.
- Mollison, D. 1986. Modelling Biological Invasions: Chance, Explanation, Prediction. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **314**:675-692.
- Molnar, J. L., R. L. Gamboa, C. Revenga, and M. D. Spalding. 2008. Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* **6**:485-492.
- Neubert, M. G. and I. M. Parker. 2004. Projecting rates of spread for invasive species. *Risk Analysis* **24**:817-831.
- NRC (National Research Council). 2002. Predicting invasions by nonindigenous plants and plant pests. National Academies Press, Washington, D.C., USA.
- Nunes, P. and A. Markandya. 2007. Economic value of damage caused by marine bio-invasions: lessons from two European case studies. Pages 775-780 in 5th International Conference on Marine Bioinvasions, Cambridge, MA.
- Nyberg, C. D. and I. Wallentinus. 2005. Can species traits be used to predict marine macroalgal introductions? *Biological Invasions* **7**:265-279.
- Nyström, P. 2002. Ecology. Pages 192-235 *Biology of freshwater crayfish*.
- Olenin, S., D. Minchin, and D. Daunys. 2007. Assessment of biopollution in aquatic ecosystems. *Marine Pollution Bulletin* **55**:379-394.
- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**:3-19.
- Paté-Cornell, M. E. 1996. Uncertainties in risk analysis: Six levels of treatment. *Reliability Engineering and System Safety* **54**:95-111.
- Persson, E. 2008. What is wrong with extinction? Doctoral thesis, Lund University, Lund.

- Peters, D. P. C. and J. E. Herrick. 2004. Strategies for ecological extrapolation. *Oikos* **106**:627- 636.
- Pimentel, D. 2005. Environmental consequences and economic costs of alien species. Pages 269-276 *Invasive Plants: Ecological and Agricultural Aspects*.
- Pimentel, D., S. McNair, J. Janecka, J. Wightman, C. Simmonds, C. O'Connell, E. Wong, L. Russel, J. Zern, T. Aquino, and T. Tsomondo. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture Ecosystems & Environment* **84**:1-20.
- Pullin, A. S. and T. M. Knight. 2009. Doing more good than harm - building an evidence-base for conservation and environmental management. *Biological Conservation* **142**:931-934.
- Quinn, G. and M. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press.
- Regan, H. M., Y. Ben-Haim, B. Langford, W. G. Wilson, P. Lundberg, S. J. Andelman, and M. A. Burgman. 2005a. Robust decision-making under severe uncertainty for conservation management. *Ecological Applications* **15**:1471-1477.
- Regan, H. M., M. Colyvan, and M. A. Burgman. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecological Applications* **12**:618-628.
- Regan, T. J., M. A. Burgman, M. A. McCarthy, L. L. Master, D. A. Keith, G. M. Mace, and S. J. Andelman. 2005b. The consistency of extinction risk classification protocols. *Conservation Biology* **19**:1969-1977.
- Rejmanek, M. 2000. Invasive plants: approaches and predictions. *Austral Ecology* **25**:497-506.
- Ricciardi, A. 2003. Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. *Freshwater Biology* **48**:972-981.
- Ricciardi, A. and J. Cohen. 2007. The invasiveness of an introduced species does not predict its impact. *Biological Invasions* **9**:309-315.
- Ricciardi, A. and R. Kipp. 2008. Predicting the number of ecologically harmful exotic species in an aquatic system. *Diversity and Distributions* **14**:374-380.

- Richardson, D. M., P. Pysek, M. Rejmanek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions* **6**:93-107.
- Sala, O. E., F. S. Chapin, III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Biodiversity: Global biodiversity scenarios for the year 2100. *Science* **287**:1770-1774.
- Schultz, C. 2008. Responding to scientific uncertainty in U.S. forestry policy. *Environmental Science and Policy* **11**:253-271.
- Shigesada, N., K. Kawasaki, and E. Teramoto. 1986. Traveling periodic-waves in heterogeneous environments. *Theoretical Population Biology* **30**:143-160.
- Shrader-Frechette, K. 1991. *Risk and Rationality*. University of California Press.
- Shrader-Frechette, K. 2001. Non-indigenous species and ecological explanation. *Biology and Philosophy* **16**:507-519.
- Simberloff, D., I. M. Parker, and P. N. Windle. 2005. Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment* **3**:12-20.
- Smith, D. L., B. Lucey, L. A. Waller, J. E. Childs, and L. A. Real. 2002. Predicting the spatial dynamics of rabies epidemics on heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America* **99**:3668-3672.
- SRA (Society for Risk Analysis). 2010. <http://www.sra.org> January 2010.
- Stohlgren, T. J. and J. L. Schnase. 2006. Risk Analysis for Biological Hazards: What We Need to Know about Invasive Species. *Risk Analysis* **26**:163-174.
- Strayer, D. L., V. T. Eviner, J. M. Jeschke, and M. L. Pace. 2006. Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution* **21**:645-651.
- Suter, G. W. I. 1993. *Ecological risk assessment*. CRC Press, Boca Raton, USA.

- Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates Sunderland, MA.
- Tversky, A. and D. Kahneman. 1974. Judgment under uncertainty - heuristics and biases. *Science* **185**:1124-1131.
- US EPA (US Environmental Protection Agency). 1998. Guidelines for Ecological Risk Assessment. Risk Assessment Forum, Washington, DC, EPA/630/R095/002F.
- Walther, G. R., A. Roques, P. E. Hulme, M. T. Sykes, P. Pysek, I. Kuhn, M. Zobel, S. Bacher, Z. Botta-Dukat, H. Bugmann, B. Czucz, J. Dauber, T. Hickler, V. Jarosik, M. Kenis, S. Klotz, D. Minchin, M. Moora, W. Nentwig, J. Ott, V. E. Panov, B. Reineking, C. Robinet, V. Semchenko, W. Solarz, W. Thuiller, M. Vila, K. Vohland, and J. Settele. 2009. Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution* **24**:686-693.
- Verhoef, G. D. and C. M. Austin. 1999. Combined effects of shelter and density on the growth and survival of juveniles of the Australian freshwater crayfish, *Cherax destructor* Clark Part 1 and 2. *Aquaculture* **170**:37-57.
- Williamson, M. 1999. Invasions. *Ecography* **22**:5-12.
- Williamson, M. 2006. Explaining and predicting the success of invading species at different stages of invasion. *Biological Invasions* **8**:1561-1568.
- With, K. A. and A. W. King. 1999. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology* **14**:73-82.