Dissertationes Forestales 57

Invasive insects in Europe - the role of climate change and global trade

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Academic dissertation

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Human induced inadvertent introductions of invasive forest insects have become a serious threat to both biodiversity and the economy, causing disturbance and direct damage to natural forests and commercial stands. The rates of forest pest invasions have increased with increased trade and travel between and within continents. There are 109 exotic phytophagous species known to have successfully invaded and established themselves on Europe’s woody plants from both North America and Asia, and more will invade as international trade continues and its volume increases (I).

Risk analysis of potential invaders is a way to prevent or suppress the number of potential invasive species. Recognition of potential invaders and their major pathways helps to prevent or reduce introductions, since not all of the imported exotic insects are invasive, nor do they manage to establish themselves in novel environments. Successful colonization is governed by several factors independent of or dependent on the invading species. The most prominent factors governing successful establishment are the ecological opportunities on arrival and the competitiveness of the invader (I, II). Suitable climate and available host species are the most prominent factors, but species abilities or life history traits, e.g. wide tolerance of hosts, asexuality and tolerance of population gaps enhance the possibility for establishment (I, II). Also the number of invading individuals, i.e. the propagule pressure may be important in increasing the probability of establishing a viable population (II).

The risk of establishment is most severe where the main host species for the potential invader occurs naturally or is widely cultivated. Climatic comparisons and simulations of climatically or biogeographically suitable areas for targeted high risk species have become increasingly important in targeting preventive or eradicative efforts where they are most needed (III, IV). Climate-based modeling tools are also helpful in determining the potential risks posed by climate change induced range shifts of native and exotic insect species (III, IV, V). Range shifts and potential population fluctuation of forest pests to outbreak levels pose a potential threat to silviculture that should be considered when planning forest management practices.

Keywords: introduced species, wood boring insect, EPPO, CLIMEX, risk analysis, Lymantria spp., poleward shift

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Joensuu, February 2008

Henri Vanhanen

LIST OF ORIGINAL ARTICLES

The thesis is based on the following articles, which are referred to in the text by their Roman numerals.

I Mattson, W., Vanhanen, H., Veteli, T.O., Sivonen, S. & Niemelä, P. 2007. Few immigrant phytophagous insects on woody plants in Europe: legacy of the European crucible? Biological Invasions 9(8): 957-974.

II Vanhanen, H., Mattson, W., Veteli, T.O., Niemelä, P. & Raffa, K. Why bark beetles with aggregation pheromone communication are poor invaders: The shackles of specialization? Manuscript.

III Vanhanen, H., Veteli, T.O. & Niemelä, P. Potential distribution ranges in Europe for *Aeolesthes sarta* (Solsky), *Tetropium gracilicorne* (Reitter) and *Xylotrechus altaicus* (Gebler), a CLIMEX analysis. Manuscript.

IV Vanhanen, H., Veteli, T.O. & Niemelä, P. Potential distribution ranges in Europe for *Ips hauseri* (Reitter), *I. subelongatus* (Motschulsky) and *Scolytus morawitzi* (Semenov), a CLIMEX analysis. Manuscript.

V Vanhanen, H., Veteli, T.O., Päivinen, S., Kellomäki, S. & Niemelä, P. 2007. Climate change and range shifts in two insect defoliators: gypsy moth and nun moth – a model study. Silva Fennica 41(4): 621–638.

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CONTENTS

ABBREVIATIONS

APHIS	Animal and Plant Health Inspection Service
DAISIE	Delivering Alien Invasive Inventories for Europe
EPPO	European and Mediterranean Plant Protection Organization
EU	European Union
IPCC	Intergovernmental Panel on Climate Change
NA	North America
PIN	Port Information Network
QPF	Quarantine Pests for Forestry
SRES	Special Report on Emissions Scenarios
USA	United States of America
USDA	United States Department of Agriculture

1. INTRODUCTION

"Jos kirva Venäjältä korjaisi viljasadon, kuoriainen Koloraadosta perunan, ei Suomessa olisi enää kansantaiteilijoita "

Though epic, the little poem holds a certain amount of truth in it. The folk artist would not die of hunger, but thrive in lack of inspiration. Exotic species seem to travel between continents nowadays, when even very exotic fruit and vegetables are brought fresh to our local stores. The speed and the growing amount of goods transported hold a threat.

Since the evolution of oxygen-producing Cyanobacteria, no single species has had such a large-scale global impact as humans. Both of the phenomena focused on in this thesis are global and are driven by economic growth: biological invasions and climate change-induced range expansions of herbivorous forest species.

Socioeconomic growth has increased the overall production of a variety of goods as well as global trade in them. This has affected the biosphere in two drastic ways, which are considered to be the greatest threats to biodiversity and to human health and institutions globally. Increased international trade has provided a way for many harmful and harmless insect species to expand their distribution beyond geographical barriers that limited their distribution in the past. When biological invasions are combined with the effects of the climate change, the formerly climatically-driven distribution ranges of animals will broaden even more. Both of these phenomena are evident and they require immediate preventive action to change previously adopted practices.

2. SPECIES DISTRIBUTION AND BIOLOGICAL INVASIONS

Today people and species are more global. The world is rapidly unifying. While wireless communication connects distant continents, we are also connected to other far away locations via global trade and travel. Together with goods and people fauna and flora move, whether intentionally or unintentionally. The distribution of a species is not a static state. It fluctuates. A species will occupy areas that are suitable for it if it is transferred beyond the barriers that have prevented its dispersal to other suitable areas. This has presented a global problem, which is firstly reviewed in this thesis through its basic concepts: species distribution and biological invasions. As this thesis is about invasive forest insects, the introductory chapters will moreover concentrate on phytophagous insects, but examples of other invasive animals or plants may be used.

2.1 Species distribution

The basic definition of species distribution is that a species occupies a unique geographic range, where the population lives and breeds (Begon *et al.* 1996 and references therein). The distribution of poikilothermic animals is determined by abiotic (e.g. climate, geographical barriers) and biotic (e.g. host plants, interspecific competition, predators, parasites, diseases) factors (Andrewartha & Birch 1954, Parmesan *et al.* 2005, Case *et al.* 2005 and references therein).

Two extreme ends of the distribution spectrum are cosmopolitan and endemic distribution. Cosmopolitan species have a very extensive distribution covering several continents, and endemic species have restricted distributional ranges on one continent or island (Begon *et al.* 1996, MacArthur 1972 and references therein).

A species distributional range is not static, but dynamic, fluctuating by dispersal of individuals or by extinction of species subpopulations (Hanski 1998, Holt *et al.* 2005 and references therein). Expanding distributional range and establishing populations in new areas require a change in abiotic or biotic factors of adjacent habitats within the population's capabilities of dispersal. Adjacent habitats may formerly have been unsuitable, or dispersal to suitable distant habitats may have been prevented by a geographical barrier, such as the sea or mountain chains. Extinction of subpopulations at the far limits of the species due to abiotic or biotic environmental changes are common. The profound goal of every species seems to be biblical: to reproduce and fill the land. To survive as a species, individuals must colonize new suitable habitats whenever a suitable window opens. Especially small meta-populations are prone to become extinct locally due to stochastic variation (Hanski 1998, Liebhold & Bascompte 2003).

2.2 Biological invasions

The introduction and spread of species outside their native indigenous distribution range, termed hereafter biological invasions, are increasing with growing world trade and tourism. Biological invasions are considered to be one of most serious threats to biodiversity (Armstrong 1995, Wilcove *et al.* 1998, Liebhold 2003) and human economics (OTA, 1993, Heikkilä & Peltola 2004, Pimentel *et al.* 2004).

Defining biological invasion is not easy, since not all of the invasive species are invasive. The term "invasive" is more or less defined by the impact of a species on a new environment or economic interests than by its capability to colonize new continents. Species that spread through human action into new areas, causing direct negative impact on the environment or economy are most often called invasive species or alien pests. Species that do not cause such an impact are more commonly called exotic, non-indigenous or non-native species. Though not having a direct negative impact, all of the species that inhabit a new continent may still alter the functioning of the ecosystem (Jenkins *et al.* 1999, O'Dowd 2003, Lovet *et al.* 2002, Holt & Lawton 1993, Koch 2003, Boettner *et al.* 2000, Vermeij 1996, Hänfling & Kollmann 2002).

Human-aided biological invasions are no new event; they have been going on ever since humans migrated to new areas. Schoolbook examples of invasive species are the introduction of *Rattus exulans* Peale by Polynesian voyagers (Atkinson and Towns 2001) and *R. rattus* L., *R. norvegicus* Berkenhout and *Felis catus* L. by European explorers, missionaries and mercantile fleets to Pacific islands (Anon. 1899, Innes 2001). The introduction of species to new areas has accelerated widely due to the increasing mobility of people and goods over the past few decades (Sailer 1978 and 1983, Niemelä & Mattson 1996, Work *et al.* 2005, McCullough *et al.* 2006). Secondly, together with the growing movement of commodities and people, the disturbance of habitats has increased the number of invasions, not by increasing the number of arrivals, but making habitats more prone to invasions (Liehold *et al.* 1995, Marvier *et al.*2004).

3. STAGES OF BIOLOGICAL INVASIONS

The process of invasion is commonly divided into separate stages for examinational purposes. These stage are referred as; **1. Arrival**, the transportation of individuals of a species to new areas, **2. Establishment**, the forming of a self-sustaining population in the new area and **3. Spread**, the expanding of distribution to contiguous suitable habitats and interaction with the surrounding ecosystem (Liebhold *et al.* 1995, Vermeij 1996, Carroll & Dingle 1996). This thesis focuses mainly on the factors that affect the second stage, i.e. the establishment phase of invasion: how abiotic and biotic factors constrain, limit or favor the establishment of a species.

3.1 Arrival – pathways and origin

The study of arrival and introduction involve the study of donor biota and regions, potential dispersers and their vectors, and pathways (Vermeij 1996). Why are some species or species from certain biota and regions good dispersers and which pathways are the most prominent for introduction?

Today, dispersal of individuals of herbivorous forest insects to a new continent or over large distances within a continent is almost always enhanced by human activities (Sailer 1978, Sailer 1983, Mattson *et al.* 1994, Humble & Allen 2001, Yan *et al.* 2001, Work *et al.* 2005). Introductions have been either inadvertent or intentional. Many arthropods are introduced with trade commodities with which they are associated, and several invertebrates and fungi have been intentionally released for biological control (Lacey *et al.* 2001, Morrison *et al.* 2005). It is not surprising that in a historical perspective, the unintentional introductions have reflected commerce and immigration patterns. As an example, parallel commerce between North America and Europe has greatly unified fauna between these continents, whereas the modes of transportation through time have reflected the fauna that arrive (Sailer 1978, Sailer 1983, Mattson *et al.* 1994, Niemelä & Mattson 1996). The movement of land arthropods in sand-ballasted frigates has changed, and now mussels are transported in water-ballasted cargo vessels.

Some species are more prone to be dispersed and introduced into new regions than others (Vermeij 1996, Niemelä & Mattson 1996), and in addition, some pathways favor immigrant insects more than others (Kiritani & Yamamura 2004, Haack 2006, Brockerhoff *et al.* 2006). In addition it has been thought that some biota or regions hold more potential dispersers (Vermeij 1996, Niemelä & Mattson 1996). The number of arriving individuals of species directly affects the size of the founder population and its vulnerability to extinction. The number of arriving individuals is called propagule pressure. Between 1985 and 2000, the United States Animal and Plant Health Inspection Service (APHIS) intercepted 500 000 insects in quarantine inspections (Haack 2006). Yearly, there are about 53 000 interceptions of non-indigenous species in the USA (Pimentel *et al.* 2000), and the number of interceptions for a species may be from one single to several hundreds per year. Recurrent introductions of species can increase the likelihood of establishing a founder population in a new area (Von Holle & Simberloff 2005, Lockwood 2005, Brockerhoff *et al.* 2006), reinforce the size of an already established population and in addition, reinforce it by bringing genetic variability to the population (Stepien *et al.* 2002, Kolbe *et al.* 2004).

3.2 Establishment

Establishment is the process of forming a persistent population. Many species are introduced so often and in such high numbers that they seem virtually persistent, but are still unable to form a locally reproducing population. An estimated 10% of inadvertently introduced immigrant phytophagous insects establish themselves, and as many as approximately 20 to 40% of intentionally introduced biological control agents establish permanent populations (Lewis & Kareiva 1993, Williamson & Fitter 1996).

By arriving in a novel distant area, the introduced species face the new abiotic and biotic constraints or opportunities, which determine the success of the species. Founder populations are often small and more prone to extinction by stochastic factors in the novel environment (Hanski 1998, Liebhold & Bascompte 2003). These factors are random incidents of population demography, environmental fluctuations, catastrophes and genetic changes in population. Thus they are driven by the before-mentioned abiotic and biotic forces in the new environment. As this thesis emphasizes these two forces enhancing or suppressing establishment, I will consider them in detail.

3.2.1 Abiotic factors

On arrival in a novel region, the introduced species will face the physical environment of the new range, which it must adapt to (Vermeij 1996, Niemelä & Mattson 1996, Holway *et al.* 2002 and references therein). At first hand the prevailing climate and landscape will determine whether the new area is habitable by the immigrant species. Generally a good match between physical factors of the donor habitat and the new habitat of the immigrant species will increase the probability of establishment. This match between distant areas is also called biogeographical similarity. Biogeography entails abiotic physical factors, such as climate and phenology defined by latitude, as well as biotic factors, which are dealt with in the next chapter.

Adaptation to the prevalent climate plays a crucial role in establishing a population in a new continent after arrival. Climate has been pointed out as a major factor affecting distribution, i.e. the survival of poikilothermic animals, in a given area (Andrewartha and Birch 1954). Seasonal climate patterns, particularly moisture and temperature, can be also crucial, especially for introduced forest pathogens. To infect suitable hosts, develop a disease and survive, correct temperature (e.g. warmer winters, milder summers) and correct moisture content (e.g. fog, rainfall, less snow cover) at a critical season are the prerequisites (Marosy *et al.* 1989).

Inability to tolerate climatic conditions and weather fluctuations in a new area is one of the main reasons for extinction of the founder population of non-native species (Crawley 1986). Albeit the immigrant population would have adapted to the prevailing climate, it is still subject to stochastic variation of weather. The average climate may favor population growth and persistence at the site, but variation of weather around average conditions can drive small populations into extinction (Elton 1924). Extreme weather events alone or several unfavorable years of weather outside average values may push non-native and also native species into extinction (MacArthur 1972, Russel 1993, Solbreck 1991).

Prevailing climate defines the seasonal phenology to which the introduced species must adapt (Vermeij 1996, Niemelä & Mattson 1996). Immigrant insects must synchronize to the annual cycle in a novel region and enter or terminate the diapause at an appropriate time to survive through the unfavorable periods of weather, for example through a cold winter, a hot summer or a dry season. Insects derive their clues about the seasonal regime from temperature and the length of the day, which both are defined by latitude.

3.2.2 Biotic factors

The rate of primary production, the amount of unused resources, anthropogenic disturbance of the habitat and low species richness have been thought to be the basic principles that make some biota more prone to invasions (Elton 1958, Vermeij 1996, Levine & D'Antonio 1999, Sher & Hyatt 1999. Davis *et al.* 2000, Byers 2002). Though generalizations exist, all biota seem to be prone to invasions. Even if the immigrant phytophagous insect can withstand the physical environment of the new region, thereafter it will face new challenges of adapting to the biotic environment, which will eventually determine its fate in establishing a founder population. The invading species requires a suitable host, its native or possible congeneric and the ability to adapt to competing species, predators, parasites and pathogens in order to establish itself (Vermeij 1996, Roques *et al.* 2006, Vercher *et al.* 2005, Mattson *et al.* 2007).

The first and foremost task in a new region is to find a suitable host (Vermeij 1996, Niemelä & Mattson 1996). If native hosts are not available it must find a taxonomically related (confamilial, congeneric) host and adapt to it. Alone, the presence of available hosts in a new region is not enough. Suitable hosts must be adequately abundant for invading insects to find them. The probability of establishment for the non-native phytophagous species depends totally on the availability and abundance of the host plants that enable larval development, and in some cases maturation feeding of imago. Strictly monophagous specialists seldom adapt to hosts that are taxonomically and chemically unrelated to their native hosts (Farrel *et al.* 1992). Rigorous host plant preferences may limit the likelihood of finding a suitable host in a new region, making generalist herbivores more presumable invaders. Specialization in turn affects the finding and selection of the host (Futuyma 1991). Many species have the ability to detect their hosts' volatile chemicals from long range (Raffa 2001, Byers 2004, Bruce *et al.* 2005). This in turn enhances the finding of the host and successful establishment in a novel environment, if the species can recognize the chemical cues.

Even if native or confamilial, congeneric, hosts were dispersed widely and abundant, the phenological synchronization of the host and the insect may be crucial for successful establishment (Vermeij 1996, Niemelä & Mattson 1996). The chemical and structural composition of the potential hosts varies during the season (Crawley & Akhteruzzaman 1988, van Asch & Visser 2007). The nutritional quality of the foliage affects the growth of larvae, and in turn, their survival (Tikkanen & Julkunen-Tiitto 2003, van Asch & Visser 2007). For this reason many herbivorous species that feed on woody plants time their larval development to synchronize with bud burst, when nutritional and soft plant tissue is available. Establishment of an invading insect may not be successful if the phenological timing is not correct with the host plant, or if the invading insect cannot tolerate less edible plant material.

When a non-indigenous phytophagous insect arrives in a new region outside its native range, it has left behind its former predators, parasites, pathogens and species that compete for the same resources. This interactive web of host-herbivore-predator/parasite/pathogen is also called the tri-trophic niche (Price 1997). On arrival, successful establishment is less likely if there is no available niche to fit, i.e. an enemy- free space with accessible hosts. A clear taxonomic difference compared to resident prey species, in other words, "camouflage" from enemies, will decrease the probability of being predated on by resident predators (Lawton & Brown 1986). Without enemy- free space, the invading insect has to escape from predation by rapid population growth and dispersal. Moreover, the immigrant species will have to face the competing species, which will reduce the growth of individuals in the introduced population and in turn affect breeding success. This could be affected by exploitation competition for shared resources, interference competition through fighting or other action, and apparent competition through a shared enemy.

3.3 Dispersal

The dispersal of an indigenous species is not only a demographic and spatial stage, but also an integration phase and evolution process between the native biota and the invader (Vermeij 1996). In extreme cases an invader may cause the extinction of a native species (Vermeij 1996, Clavero & García-Berthou 2005) or a native species may drive the invader to extinction (Lawton & Brown 1986). This integration of the invader with the surrounding biota is discussed more thoroughly in the next chapter.

The process of spread is the only part of the invasion that can be clearly observed, followed and studied. Many introduced species are not detected due to the small size of the founder population (Liebhold & Tobin 2006). They are rarely caught in connection with routine surveillance trappings of insects. Introduced species are noticed after a population grows to detectable levels (Liebhold & Tobin 2006). A good example of non-detection of the arrival and establishment of a non-indigenous species is the discovery of an Asian bark beetle Scolytus schevyrewi in the USA (Negrón *et al.* 2005, Haack 2006). The species was discovered for the first time in spring 2003 in insect traps set in Denver, Colorado. By fall, it was found in fourteen other states, and closer examination of old insect collections revealed that the insect had already been collected in Colorado in 1994 and in New Mexico in 1998.

Spread involves population growth and dispersal of individuals of the species (MacArthur 1972, Liebhold & Tobin 2006). With an increase in density, the species will disperse and expand its range to adjoining areas of suitable habitat. Species differ in their ability to disperse. Individuals of sedentary species diffuse to adjoining areas when the density of the founder population increases and less sedentary species may disperse several kilometers, independent of population density (Tobin *et al.* 2004). After establishing a founder population, individuals may also be transported deliberately by human aid inside new region or continent and form new dispersal centers.

By expanding to a larger area, the species furthermore decreases its probability of becoming extinct. Species that inhabit large geographic ranges and occur abundantly locally are often less affected by stochastic changes in demographics, population genetics, and in the environment, or as a result of catastrophes (MacArthur 1972, Leigh 1981). By contrast, are the species that are consistently sparse and their distribution is geographically restricted. With expansion, the species will face the same biotic forces as in establishment. New communities will have to integrate if no free niche is available.

4. IMPACTS OF BIOLOGICAL INVASIONS

As already mentioned, the dispersal phase usually involves the integration of the invader with the surrounding biota. Invasive species may have an ecological impact on native species. The impact may occur on ecosystem, community, population, individual, or genetic level (Liebhold 1995, Vermeij 1996, Hänfling & Kollmann 2002). The phytophagous invader may have an impact on the recipient environment, e.g. by altering nutrient cycling (Jenkins *et al.* 1999, O'Dowd 2003, Lovet *et al.* 2002) through intensive leaf consumption. It may also change the predation/parasitism/herbivory regime (Holt & Lawton 1993, Koch 2003, Boettner *et al.* 2000), change competition between species (Goulson 2003) and vector new pathogens (Goulson 2003, Jacobi *et al.* 2007). The invader may also hybridize with close relatives (Brasier 2001) and also cause direct disturbance or destruction of a habitat (Liebhold *et al.* 1995, Byers 2002). These all have a huge impact on the diversity of life, from ecosystem to single gene level.

Invasive species may directly exclude native species (Goulson 2003), change community structure (Liebhold *et al.* 1995) and function (Lovet *et al.* 2002) or affect population genetics in the recipient community (Hänfling & Kollmann 2002). The chestnut blight (*Cryphonectria parasitica* Murril) that was accidentally introduced from Asia to North America had all these afore-mentioned dimensions when it spread and killed almost all the chestnut trees (Castanea spp.) in North America, a tree species that was previously dominant before the arrival of the pathogen. It almost eradicated one single species from North America and changed the community structure since chestnut trees were replaced by oaks (Quercus spp.) (Liebhold *et al.* 1995 and references therein). This change in forest composition created by Chestnut blight favored another invasive species, an insect defoliator. The Gypsy moth (*Lymantria dispar* L.), which uses oaks as its main host species. The change inflicted by these two invaders, Chestnut blight and Gypsy moth, may have altered the genetic structure of communities and individuals in the recipient biota by changing the direction of selection, although such outcomes are hard to detect and trace.

5. CLIMATE CHANGE AND BIOLOGICAL INVASIONS

Global mean surface temperature has increased by 0.4 – 0.8°C over the 20th century (IPCC 2001). Anthropogenic influence on the atmosphere through increased concentrations of greenhouse gases (i.e., carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), tropospheric ozone (O_3)) and aerosols has induced a climate change that affects biomes globally (Thomas *et al.* 2004, Parmesan 2006). The globally averaged surface temperature is projected to increase by 1.4 – 5.8°C by the year 2100 (IPCC 2001). The estimated increase is based on the A1, A2, B1 and B2 emission scenarios by the Intergovernmental Panel on Climate Change, abbreviated IPCC (IPCC 2001). The scenarios differ in the way they predict socio-economic growth (demographic, social, economic, and technological) worldwide and the scale of future emissions based on it.

The most prominent impact of climate change on biological invasions will be to make invasions of exotic forest pests from southern locations to northern ones more prevalent. The summer and winter temperatures are not likely to increase in an equal manner. In the boreal zone, winter temperatures are expected to rise more than summer temperatures (IPCC 2001). By raising winter temperatures that are lethal to many southern species, climate change will enable the survival of native and exotic species from more southern locations.

On a general basis, climate change will have two kinds of effect: direct effects on the physiology of herbivorous insects and indirect effects mediated through its host plants. Indirect effects of change have been noted to alter the behavior of insects and their hosts empirically and in experimental trials. The change may be either phenological, affecting the synchrony between the host and the herbivorous insect or physiological, affecting the quality of the host on which the herbivore feeds (Bezemer & Jones 1998, Veteli *et al.* 2002, Bale *et al.* 2002, Battisti 2004 and references therein). Climate change will also have direct effects on insect performance and behavior. In particular, increased temperatures will allow many species to expand their distributional ranges polewards or to higher altitudes (Parmesan *et al.* 1999, Thomas *et al.* 1999, Thomas *et al.* 2001, Walther *et al.* 2002, Root *et al.* 2003, Battisti 2004, Battisti *et al.* 2005, Battisti *et al.* 2006, Hickling *et al.* 2005), but they will also cause outbreaks more frequently (Virtanen *et al.* 1995, Williams & Liebhold 2002), especially by lowering lethal winter temperatures (Crozier 2004, Battisti *et al.* 2005, Veteli *et al.* 2005, Robinet *et al.* 2007), allowing more rapid development (Williams *et al.* 2003) and the production of more generations during a growing season (Hansen *et al.* 2001, Lange *et al.* 2006), and indirectly making host trees more prone to attack, e.g. by drought (Solberg 2004, Rouault *et al.* 2006, Schlyter *et al.* 2006).

6. PREDICTING AND PREVENTING INVASIONS

Besides their direct and indirect impacts on native ecosystems, invasive species cause immense economic losses. In the USA there are over 50 000 non-native species, and the economic losses which invasive species cost are almost $ 120 billion per year in prevention and damage control (Pimental *et al.* 2004). In China there are 283 invasive non-indigenous species, which caused $ 14.45 billion worth of economic losses (Callaway *et al.* 2006). Due to their impacts on economics and native fauna and flora, efforts are being made to prevent the unintentional introductions of non-native species.

Efforts to prevent the introduction of invasive species include quarantine regulations, inspections of imported goods and actions based on risk analysis, which are usually made for high risk species. Risk analysis is usually based on potential pathways and vectors. It estimates the likelihood of the invader to establishing itself and becoming invasive according to biogeographical (climate, habitat, hosts) suitability. Also, the consequences and economic losses after establishment are sometimes estimated in risk assessment. This knowledge will further be valuable when forming management strategies and policies to prevent invasions or to suppress damage by invaders.

6.1 Tools for risk analysis and prediction

Prediction tools are usually based on the climatic suitability of the area for the potential invader and sometimes on the comparison of donor and recipient biota or an estimate of free niches by niche-based modeling.

Biogeographical similarity between donor and recipient areas have been thought to be one of the most crucial issues affecting invasions of insects; this includes corresponding climate, habitats, hosts and phenological similarity (Gibbs & Wainhouse 1986, Niemelä & Mattson 1996, Vermeij 1996, Mattson *et al.* 2007). The finding that distribution of insect species is ultimately determined and altered by climate (Andrewartha and Birch 1954) has been used to determine the potential distribution ranges of potential invaders by Geographical Information System (GIS-based modeling programs or quantitatively based analyses of temperature thresholds and critical temperature values (Sutherst & Maywald 1985, Thomas *et al.* 1999, Baker *et al.* 2000, Sutherst *et al.* 2000, Williams & Liebhold 2002, Crozier & Dwyer 2006).

There is also an increasing number of GIS-based habitat models for estimating the risk of potential invaders (Thomas *et al.* 1999, Baker *et al.* 2000, Kalkhan & Stohlgren 2000, Thuiller *et al.* 2005), which are moreover aimed at evaluating the potential of exotic plants to invade a certain habitat.

Provided the climatic requirements are met, the invading species requires a suitable host for successful establishment. Host availability estimation is crucial when herbivorous insects are considered, and therefore palatability tests are conducted or estimates are made of suitable hosts for the most invasive pests (MacFarlane & Meyer 2005, MacLeod 2002). The availability of native hosts and the palatability of congeneric species in the recipient region are determinants of the species' potential to establish itself and invade a region. Possible relationships between native predators, parasites and potential competing species are difficult to estimate and they are often neglected in risk assessments.

6.2 Intergovermental and govermental organizations

The palette of organizations working with invasive species in the intergovernmental sector is very colorful. Several intergovernmental organizations develop strategies and try to unify regulations to prevent the introduction and spread of invasive species worldwide. At the other end of the spectrum are the national agencies that try to protect national nature reserves and the economy from the potential introduction of a pernicious pest species. Two very different organizations are presented in the next chapters. Both of them work with the same issue, invasive non-native species, but at different levels. One is an intergovernmental organization that works between nations and their phytosanitary agencies, and the other works on a national basis to prevent introductions of alien species by inspections and eradication programs.

6.2.1 European and Mediterranean Plant Protection Organization and quarantine pests for forestry

The European and Mediterranean Plant Protection Organization (EPPO) is an intergovernmental organization that coordinates European plant health and phytosanitary issues. Its approach is to develop international strategies for preventing the introduction of plant pests and diseases and to search for efficient control methods.

In order to assess the risk from new exotic wood boring insects, EPPO started a project in the year 2000 with the purpose of estimating the potential risks associated with the timber trade in the EPPO region and preparing diagnostic protocols for the regulated pests of the EPPO region and the European Union (EU) Member States (Orlinski 2006). Special emphasis was placed on the risk involved in timber imported from Russia and the former

Soviet states. A total of 1365 potential pest species were estimated in the project, and 19 of them were recommended for addition to the EPPO lists of pests recommended for regulation, “Quarantine Pests for Forestry” (QPF).

Phytosanitary inspections of coniferous wood imported from Russia and the former Soviet states to the EU started on March 1, 2005, in connection with the QPF list and Commission Directive 2004/102/EC. Inspections were aimed at minimizing or eliminating the phytosanitary threat and protecting commercial stands and other forests within the EU from pests such as *Bursaphelenchus xylophilus* (Steiner & Bührer) and *Dendrolimus sibiricus* (Tschetverikov) associated with imported coniferous wood. Phytosanitary inspections were aimed especially at detecting the species of the EPPO A2 list, a list of quarantine pest that are locally present in the EPPO region.

6.2.2 Animal and Plant Health Inspection Service and the Port Information Network

Unlike EPPO, the Animal and Plant Health Inspection Service, APHIS is a governmental agency, which is operated by the United States Department of Agriculture (USDA). Its primary goal is to protect the agricultural and natural resources of the United States (USA). Furthermore its aim is to prevent introductions of invasive non-indigenous animals, plants and pathogens. APHIS also monitors and coordinates eradication and management for those invasive non-native pests already present.

Being responsible for executing the quarantine inspections, APHIS has gathered information on intercepted plant pests at United States ports of entry (Work *et al.* 2005, McCullough *et al.* 2006). This database is called the Port Information Network, PIN database. The PIN database has been maintained since 1985, and it gathers approximately 53 000 interceptions per year. The database enables the projection of historical trends in pathways, species and quantities of introduced species, and furthermore assists in developing strategies for preventing introductions.

7. AIMS AND METHODS OF THE STUDY

The objectives of this thesis were:

I. ***to present a comprehensive checklist of the exotic phytophagous species known to have successfully invaded and become established on Europe’s woody plants, from both North America and Asia***
II. ***to find out if species with elaborate pheromone communication systems coordinating their aggregation and mass colonization attacks in their native systems are less successful in the invasion of a novel ecosystem than species lacking these systems***
III. ***to resolve whether quarantined species from the EPPO A2 list, could establish viable populations in Europe and how would they react to changes in climate***
IV. ***to simulate how climate change could affect the range and distribution of native insects***

The aim of objective I was approached by comprehensively deriving information on invasions from many diverse sources of the forestry, agricultural, and taxonomic entomological literature covering the past 100 or so years. Knowledge is cumulative, an insect that was identified as non-native in the mid-19th century is generally recorded as such in every checklist published since then, unless taxonomic revisions have been made. There are no fully up-to-date published or internet-based checklists for Europe except DAISIE (Delivering Alien Invasive Inventories for Europe), which is still being constructed, and therefore the search included authoritative surveys, reviews, checklists (Fauna Europea 2005), and special journal articles (e.g. EPPO, EBSCO, KLUIWERT), as well as national databases. The aim, besides that of constructing the list was to compare the invasive species in Europe with the data on European species established on woody plants in North America, and to propose some likely explanations for the vast imbalance in invasive species numbers between the two continents.

In objective II, the interception frequency data on bark and ambrosia beetles (Coleoptera: Scolytidae) from the PIN database of APHIS, as summarized in articles by Haack (2001, 2006), was used to test which factors affect the successful establishment of the species. The inspected quantity of international cargo that enters the USA is only 2%, and inspection and reporting systems are mainly targeted at high risk cargo, pathways and organisms, in other words, at those species that attack living plant material. In the case of ambrosia beetles, which attack only dead trees, they are more likely to be dismissed without reporting than bark beetles, which attack live trees. This creates an unfortunate and unavoidable bias to the data. All species that feed on fruits and seeds of trees and shrubs were excluded from the analyses; only the wood boring bark and ambrosia beetles were included. The records used comprised 2674 interceptions of 100 different bark and ambrosia beetles. Of these species 46 have established populations in the USA. Because the PIN data is biased towards the interception of high risk species attacking live trees, thus excluding many ambrosia beetles, the species that were known as established in North America (NA), but not reported in the interception records, were first removed from the statistical testing. In the second analysis, all of the species were included, whether or not there were PIN interception records of them. Nominal logistic regression was used to analyze which factors explain the probability of the species becoming established in the USA. The objective was to focus primarily on the importance of innate host finding and colonizing strategies, and secondarily on breeding strategies or interception rate as predictors of invasion success.

In objective III the potential distributions for three bark beetle species (Coleoptera: Scolytidae): *Ips hauseri*, *I. subelongatus* and *Scolytus morawitzi* and three long horned species (Coleoptera: Cerambycidae); *Aeolesthes sarta*, *Tetropium gracilicorne* and *Xylotrechus altaicus* from the Eppo A2 list were simulated with CLIMEX. The physiological parameters used in modeling were based on reviews of Russian entomological literature (Eppo 2005a, b, c, d, e, f and references therein). The literature did not cover all of the needed physiological parameters, and therefore the final fitting was carried out by estimation on the basis of the species' current distributions and seasonal phenology as an iterative geographic fitting procedure.

The simulations were based on climatic factors only, and other factors that might affect the possibility of these species becoming established in Europe, such as potential host species, were discussed briefly and speculatively. Together with potential distribution prediction, the possible distribution of these species by climate change was also considered. The SRES (Special Report on Emissions Scenarios) emission scenario A1B (IPCC 2001) was used in this study of the various climate change scenarios. According to the A1B scenario, the global mean temperature will rise by approx. 2.9°C by the year 2100.

In objective IV, the range and distribution of two important lepidopteran forest defoliators, the Nun moth (*Lymantria monacha*) and the Gypsy moth (*Lymantria. dispar*) were simulated with CLIMEX-modelling software, with and without climate change scenarios. The parameter values used in the study were derived from the literature, and the final fitting was done by estimation on the basis of the species' current distributions and seasonal phenologies in Europe (Distribution maps of insect pests 1955, Schwenke 1978, Distribution maps of insect pests 1981, Carter 1984, Marttila *et al.* 1996, Hulden *et al.* 2000, Hydén *et al.* 2006) as an iterative geographic fitting procedure.

The analysis is biased towards the species' potential to be significant defoliators in Northern Europe as a result of climate change, using IPCC´s third assessment report on climate change. The globally averaged surface temperature is projected to increase by 1.4 – 5.8°C by the year 2100, based on the A1, A2, B1 and B2 scenarios (IPCC 2001). The scenarios differ in the way they predict socio-economic growth and new technologies. In this study, the potential geographical ranges are simulated using three different temperatures varying within these limits: 1.4, 3.6 and 5.8°C.

8. RESULTS AND DISCUSSION

8.1 Checklist of nonnative species in Europe and species characteristics in establishment

We listed 109 exotic phytophagous insects that have invaded and established populations in Europe. 57 of them are from North America (NA) and 52 from Asia (A). Four orders account for about 84% of the immigrants: Homoptera 39%, Lepidoptera 13%, Coleoptera 19%, and Hymenoptera 13%. The majority of these invasive species (63% of NA and 77% of A) live on deciduous trees, of which 36% have been introduced from NA and Asia. The remaining insect species (37% NA and 25% A) live on various conifers, of which 53% have also been introduced. Most (57%) of the NA insects feeding on coniferous plants live on their introduced, native host plants. Lists are never static since new species are continuously arriving and populations of those already established may die out ??due to the stochastic nature of small founder populations (Hanski 1998, Liebhold & Bascompte 2003).

As previously discussed, establishment is governed by suitability of climate, i.e. biogeographical similarity, but also by (1) species richness/abundance in donor population and recipient population, (2) propagule pressure, (3) ecological opportunities on arrival (level of primary production, hosts, enemies, etc.) and (4) the ecological competitiveness of invaders (Sailer 1983; Spence 1990; Vermeij 1991; Niemelä and Mattson 1996 and references therein). Various studies have been made attempting to resolve the ultimate factor for invasiveness. When we listed the immigrant insects in Europe to date and their host plants, and then compared the number of phytophagous insects that have invaded the US from Europe, we found the same biased insect trade pattern that Niemelä and Mattson (1996) discovered. There are over threefold more European invasive phytophagous insects in the US than vice versa, though number of immigrant insects has increased by 13% in the US and 40% in Europe since Niemelä and Mattson's 1996 article. On the basis of comparative analysis, the most likely explanation for biased invasiveness were the two latter explanations: 3. Ecological opportunities on arrival through availability, abundance and quality of hosts, number of competitors and enemies and 4. Ecological competitiveness of invader through evolutionary history of the species, e.g. tolerating wide-amplitude population fluctuations, adoption of favorable photoperiod and thermal regime synchrony.

The data suggest that many NA immigrant phytophagous species in Europe have been successful in establishing permanent populations because their native hosts preceded or accompanied them into Europe and/or were asexually reproducing species. Fewer invasive phytophagous insects may have become established in European compared to North American woodlands because of the unique legacy of the European Pleistocene/Holocene crucible (i.e. endless cycles of populations contracting into highly disparate, dispersed metapopulation refugia and eventually expanding out of them), and the greater anthropogenic impact on European species and ecosystems that caused highly diminished heterogeneity (Niemelä & Mattson 1996). This translates into fewer and less penetrable tri-trophic niches in Europe due to the lower numbers and availability of host plants, but at the same time the higher zootic resistance per niche deriving from more competition-hardened competitors and possibly more natural enemies. Moreover, many European species are probably superior invasion specialists due to the crucible-favored traits that are conducive to success in highly subdivided and extinction-prone metapopulations: asexual reproduction, polyploidy, and other traits especially conducive to persistence under stress and explosive growth/spread under amelioration.

The ecological competitiveness of invaders hypothesis was also one of the explanatory factors for invasiveness, when the number of interceptions and establishments of bark and ambrosia beetles in the US was compared and tests were conducted to find out whether the invasive species' host colonization behavior (population aggregation pheromone signaling) and reproductive traits (out- vs. inbreeding) substantially affect their ability to establish populations. Propagule pressure has earlier been suggested by Brockerhoff *et al.* (2006) as an explanation for the probability of successful establishment by invasive bark beetles, but evidence is so far weak.

Out of the 46 bark and ambrosia beetle species that have become established in the US, only 12 (26%) are true bark beetles. Seven (15%) species of the newly established species use aggregation pheromones for orientation and are also sexually breeding. Thirty-nine (85%) of the established species do not use such pheromones. Of these, seven (18%) are sexually breeding.

The study demonstrated that there is a significant positive relationship between beetle establishment and interception numbers. Furthermore, the analyses also strongly suggested that species not employing aggregation pheromones are much more likely to establish themselves than those using pheromones. In addition, species having some form of asexual reproduction were more likely to become established than purely sexual species, at least in the full data set comprising all of the intercepted bark and ambrosia beetles. In the reduced data set comprising species found only in PIN interceptions, breeding strategy was not statistically significant. However, it is known that 37 out of 50 established invasive bark and ambrosia beetles are capable of asexual reproduction.

The analysis suggests that beetles that employ population aggregation pheromones in tree colonization are apparently less successful invaders than those that colonize trees without such aggregation pheromones, though many of the former are considered highly evolved, aggressive, tree killing species. Also, species capable of asexual reproduction, and sib mating were apparently more successful invaders. Although many pheromone signaling bark beetles are frequently and abundantly intercepted, they have seldom established invasive populations on novel hosts. The results presuppose that such bark beetles are typically poorer invaders because they and their rich coterie of mutualistic symbionts form a complex community, whose physiology and behavior is so closely chemical co-evolved with one another and their ancestral host trees that it constrains their potential colonizing opportunities to very close host congeners not usually found in distant novel environments.

8.2 Risk assessment based on climate modeling

Adapting to prevalent climate plays a crucial role in establishing a population in a new continent after arrival in a novel region or continent. We found that all of the studied EPPO A2 – QPF listed wood boring insects, *A. sarta, T. gracilicorn*e, X. altaicus, I. hauseri, I. subelongatus and *S. morawitzi*, had a potential for establishment in Europe according to climatic suitability.

For only one of the species simulated, *A. sarta*, did our model project difficulties in establishing populations in the central and northern parts of Europe. All of the other species had potential to establish themselves practically anywhere in Europe except the most southerly parts, which again were suitable for *A. sarta*.

Climatic and CLIMEX-model based pest risk assessments have been criticized for dismissing other factors that affect the probability of establishment, such as range of host plants and potential predators, and parasites. Criticism of this methodology has been presented by many researchers (e. g. Davis *et al.* 1998; Samways *et al.* 1999), while others claim that, when adequate data for the species studied are missing, this method may be the only choice available (Baker *et al.* 2000). On the other hand, knowledge of the bioclimatic suitability of an area for the pest provides information on its establishment potential, since the distribution of poikilothermic animals is ultimately determined by climatic factors (Andrewartha and Birch 1954). Together with distributions of potential host trees, simulated models of potential distribution constitute the first stage in pest risk assessment.

Lack of native or congeneric host plants has been shown to limit the establishment of exotic herbivore insects (Niemelä & Mattson 1996, Roques 2006), but favorable climatic conditions, and also the presence of host trees in many of the European forests, commercial stands and in urban areas, make establishment possible for the studied species. Distributions of hosts for the studied species are not continuous, and these discontinuities will limit and slow down spreading if they become established in Europe. It is, however, unlikely that the establishment of these species would be inhibited by lack of suitable host trees.

There is as yet no evidence of the successful establishment of any of the studied species in Europe, but *I. subelongatus, T. gracilicorne* and *X. altaicus* have been intercepted in phytosanitary inspections within Europe (Siitonen 1990, Krehan & Holzschuh 1999). Only *A. sarta* has been reported as introduced in Europe (Oelschläger 1971). The species was found in field survey in Austria, but it has not established itself.

8.3 Effect of climate change on native and potential invasive species

Both of the studied native European Lymantriid species reacted by a northward shift of distribution range when tested with IPCC´s (2001) three different climate change scenarios. The climate warming scenarios shifted the northern boundary of the distribution for both of these species north by approx. 500–700 km. The southern edge of the ranges also retracted northwards by 100–900 km. The summer and winter temperatures are not likely to increase in an equal manner. In the boreal zone, winter temperatures are expected to rise more than summer temperatures (IPCC 2001). Even though we did not consider the winter and summer temperature changes separately, as Crozier and Dwyer (2006) did in their analysis with *Atalopedes campestris* (Lepidoptera: Hesperiidae), the range shift was remarkably similar to that presented in their study. These range shifts are also remarkably similar to empirical findings of Parmesan *et al.* (1999), which analysed the geographical ranges of butterfly species and found that of 35 analysed species, the northern boundaries of 22 species had shifted northwards by 35 to 240 km while 2 had shifted southwards during the last century. Furthermore, an analysis of 51 species of British butterflies showed that 11 species had expanded their range in the northern part of their distributional range (Hill *et al.* 2002). Other data supporting the hypothesis that winter warming in particular is driving insect range expansion to the north were found by Walther *et al.* (2002), Crozier (2004) and Battisti *et al.* (2005).

The processes for these margin changes in ranges may be both ecological and evolutionary. If abiotic factors such as temperature allow, habitat breadth can be increased as well as dispersal tendencies, which may result in extraordinarily rapid dispersal into new areas across habitat disjunctions that would have constituted barriers to dispersal (Thomas *et al.* 2001). For the studied species, the poleward shift could be relatively slow, since they are fairly sedentary, occasionally reaching outbreak densities in core areas of their distribution (Schwenke 1978, Bejer 1988, Maksimov, S. 1999). However, the rates of local extinctions and colonizations within the margins of their range may be quite rapid (e. g. Parmesan *et al.* 1999, Thomas *et al.* 2001).

The studied EPPO A2 – QPF listed wood boring insects responded to climate change scenarios like the two studied Lymantriid species, by a shift of the northern boundary of their potential distribution in Europe. The range shift varied from 200 to 1100 km. On the whole, climate change will make biological invasions of species from southern locations more prevalent, especially by raising lethal winter temperatures. As almost all of the studied species are already capable of inhabiting practically any part of Europe, climate change would only have an effect on the species if they were already established in Europe. In that case climate change would appear as a range shift, or as suggested generally for wood borers and bark beetles, it would become more detrimental, as the prolonged growing season would lead to multivoltinism, in the absence of extreme temperatures in winter that diminish population levels and possible shifts to novel host plants (Liebhold *et al.* 1995; Ayres and Lombardero 2000, Volney and Fleming 2000, Battisti 2004, Veteli *et al.* 2005, Battisti *et al.* 2006, Stastny *et al.* 2006).

9. CONCLUSIONS

Human-induced inadvertent introductions of invasive forest insects have become a serious threat to biodiversity and the economy, causing disturbance or direct damage to natural forests and commercial stands. The rates of forest pest invasions have increased with increased trade and travel between and within continents. There are 109 exotic phytophagous species known to have successfully invaded and established themselves on Europe’s woody plants, from both North America and Asia, and more will invade as international trade continues and its volume increases.

Risk analysis of potential invaders is a way of preventing or suppressing the number of potential invaders. Recognition of potential invaders and their major pathways help to in prevent or reduce introductions, since not all of the imported exotic insects are invasive, nor manage to establish themselves in novel environments. Successful colonization is governed by several factors independent of or dependent on the invading species. The most prominent factors governing successful establishment are the ecological opportunities on arrival and the competitiveness of the invader. Suitable climate and available host species are the most prominent factors, but species abilities or life history traits, e.g. wide tolerance of hosts, asexuality and tolerance of population gaps, enhance the possibility of establishment. Also, the number of invading individuals, i.e. the propagule pressure, may be important in increasing the probability of establishing a viable population.

The risk of establishment is most severe where the main host species for the potential invader occurs naturally or is widely cultivated. Climatic comparisons and simulations of climatically or biogeographically suitable areas for targeted high risk species have become increasingly important in targeting preventive or eradicative efforts where they are most needed, as we found the possibility of six EPPO A2 – QPF listed wood boring insects, *A. sarta, T. gracilicorne, X. altaicus, I. hauseri, I. subelongatus* and *S. morawitzi,* to become established in Europe. Even though the impact of the exotic species in a novel environment is always something of a guess, risk assessment evaluations lose their meaning if they are ignored.

Climate-based modeling tools are also helpful in determining the potential risks posed by climate change-induced range shifts of native and exotic insect species, although they do not allow consideration of possible changes in bottom-up or top-down regulation of the populations. These factors include e.g. resource availability, diseases, parasites and predators. Nonetheless, range shifts and potential population fluctuations of forest pests to outbreak level pose a potential threat to silviculture. This threat should be considered when planning forest management practices, as many other potential pest species are likely to migrate further north than the Lymantriid species studied here.

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