SPATIOTEMPORAL DYNAMICS OF INTRODUCED BARK BEETLES

Bjørn Økland[1], Olav Skarpaas[2], Kyrre Kausrud[3], Nils Chr. Stenseth[3], Nadir Erbilgin[4]

[1]Norwegian Forest and Landscape Institute, P.O.Box 115, N-1430 Ås, Norway
[2]Norwegian Institute for Nature Research, Gaustadalleen 21, NO-0349 Oslo, Norway
[3]Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, P.O.Box 1050 Blindern, N-0316 Oslo, Norway
[4]Nadir Erbilgin,140 Mulford Hall, Division of Organisms and Environment, University of California, Berkeley CA 94720

Biological invasions cause serious ecological and economic impacts around the world (D'Antonio and Kark 2002, McGrath and Farlow 2005, Pimentell 2002). Once alien pest species have become established in their new habitats, they may be extremely difficult to eradicate, and the costs of damages and control programmes may be very high. In many cases the damage caused by the invading organisms is more serious in the new range than in the native range of the pest (e.g. *Dendroctonus valens* in China). In Scandinavian forests, the native spruce bark beetle *Ips typographus* causes significant economic damage on Norway spruce. The last outbreak of this species in Norway (1971–1981) killed the equivalent of 5 million m^3 of spruce timber within a 140,000 km^2 area (Bakke 1989).

A few years ago, a close relative of *I. typographus*, the non-native eight-toothed spruce bark beetle (*Ips amitinus*), was found in bark samples from imported Russian and Baltic timber (Økland 2002, Thunes *et al.* 2003). More recently, the first hibernating individuals of *I. amitinus* were trapped at a timber storage site in Southern Norway, in which large amounts of Baltic timber had been stored up to 2003 (Fig. 1). However, all of the timber was removed in 2004 when we conducted a trapping using synthetic pheromones in a gradient from the storage centre and out to the surrounding forest (Økland *et al.* 2005). We used *I. typographus* pheromones in the traps, because *I. amitinus* attractants (Amitinuswit) were not delivered prior to the major flight season of this pest. We used pheromones of *I. typographus* because it consists of 3 compounds, *S-cis*-verbenol, 2-methyl-3-buten-2-ol and ipsdienol and some of these compounds, such as ipsdeinol, may be attractive to *I. amitinus*. Even with this less effective attractant, we captured three individuals of *I. amitinus*, which most probably emerged from their hibernation in the ground below the timber. We suspect that the density *I. amitinus* in the traps would probably have been much higher with a specific pheromone for this species. During the swarming season, the total density of all bark beetles (mainly *I.*

Figure 1. The first records of hibernating *Ips amitinus* in Scandinavia were done in this timber storage in southern Norway. Note the close distance to surrounding forests

typographus) was about an outbreak level in the central traps and declined with distan*cet al.* 2005); however, other intermediate timber storages are still in use.

Knowledge about the spread of new bark beetle species is critical because of their ecological and economic impacts on native renewable resources. Aggressive bark beetles are some of the most destructive insects in temperate conifer forests and kill virtually all susceptible host trees over extensive areas during outbreaks. Many of these species are not currently present in Scandinavia, such as *Dendroctonus ponderosae* and *D. frontalis* that killed pines equivalent to about 50 million m^3 in the period 1979–1983 in the USA (Hoffard 1985, McGregor 1985). Other harmful bark beetle species, such as *D. rufipennis* and *I. pertubatus* in Alaska, could potentially amplify the outbreaks of *I. typographus* if they were introduced into Scandinavian spruce forests (Bright 1976, Furniss and Carolin 1977, Werner and Holsten 1997, Wood and Van Sickle 1992,

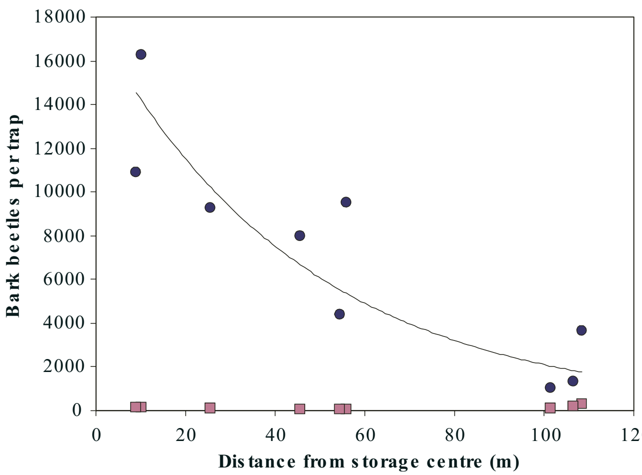

Figure 2. Density of bark beetles per trap plotted against distance from the timber storage centre. Trapping periods were 22 April – 14 May (circles) and 14 May – 13 July (squares). Modified figure from Økland *et al.* 2005

Wood 1982). Another bark beetle species, *I. cembrae*, is known as an aggressive and damaging species in Central Europe and Asia, while a very close relative, *I. subelongatus*, is considered the most important xylophagous pest in Siberia and the north-eastern part of European Russia. In Denmark, *I. cembrae* has been spreading since its discovery in 1995, and the damage associated with this insect is serious (Harding *et al.* 1996).

In addition to preventive measures that aim to stop the arrival of invasive species, insight into the spatiotemporal dynamics of introduced species is a necessary part of understanding how new species spread and get established in new habitats. Unfortunately, the detection of invasive species usually lags several years behind their arrival (Shigesada and Kawasaki 1994). Successful efforts in forest management to prevent establishment of new species are dependant on a well-developed ecological theory for these systems. Several novel aspects of ecological theory of relevance to management will be explored in the present project. First, while much of ecological theory on population cycles and outbreaks invokes predation as the driving force (Begon *et al.* 1986, Krebs 1978), the population dynamics of bark beetles are resource-driven (Økland and Berryman 2004, Økland and Bjørnstad 2006). Second, the resource dynamics of bark beetles are highly stochastic. Most studies of resource exploitation and competition are based on mean-field theory, often leading to simple dynamics. In contrast, stochastic resource dynamics may lead to complex fluctuating patterns that are intermediate between cycles and chaos (Økland and Bjørnstad 2006). Third, the outbreak dynamics of bark beetles may be driven by a particular kind of resource dynamics that has received little attention in general ecological theory: when bark beetles reach a threshold density, they switch from their standard resources, such as dead or windfelled trees, to attacking and killing standing, apparently healthy trees (Berryman 1982, Økland and Berryman 2004). In this way, the organism essentially creates its own habitat and exploits an additional resource when the population reaches high densities. Finally, while we have begun to explore some of these issues in ongoing non-spatial analyses (Økland and Bjørnstad 2006), the spatial dynamics of these systems are completely unknown.

The spatial dimension has been shown to be fundamental to the dynamics in a number of systems, with important implications for management. Understanding the mechanisms behind spatio-temporal patterns of spread may be crucial to predict rates and patterns of spread, and assess how the management should act. Spatio-temporal dynamics ranging from frozen hotspots to waves, spirals and chaos can be generated in relatively simple systems (e.g. coupled map lattice models, Bjørnstad and Bascompte 2001). Spatially synchronous dynamics have been predicted by simulations and observed in several natural systems (Johnson *et al.* 2004, Bjørnstad *et al.* 2002), including *I. typographus* in Norway (Økland and Bjørnstad 2003). The niche overlap between bark beetles is known from several empirical studies (e.g. Nuorteva 1968). Theory predicts that spatial synchrony can be generated by three main mechanisms, dispersal, interactions and external forcing (Bjørnstad *et al.* 1999), and that the degree of synchrony depends on the strength of these forces. However, it is unclear how robust these generalizations are to non-linearity, threshold dynamics and spatial heterogeneity. This raises a number of questions that can be addressed in the bark beetle system. For instance, what patterns do such systems generate? How do the patterns, in particular outbreak patterns, change with respect to dispersal, degree of niche overlap and external forcing by climate? Are the fundamental aspects of the non-spatial single-species dynamics of the native bark beetle retained with the introduction of another species? What are the implications for management?

In a new project from 2006 to 2008, we will study the potential spread of introduced bark beetles, and evaluate their impacts on the spatiotemporal dynamics of the native spruce bark beetle. We will use an integrated approach that includes mathematical models and various aspects of ecology of bark beetles. Since experimental introductions of new species would be potentially very harmful, we will investigate these questions by a combination of mathematical models and time series analyses of population data. We will approximate an experimental situation using time series analysis and spatially explicit and realistic models based on existing time series of bark beetle observations and realistic landscape structures in a geographic information system (GIS). We will validate the model using patterns of spread of invasive bark beetles in other countries. Subgoals of the project are:

1. Develop a spatially explicit model for the native spruce bark beetle *Ips typographus*, and optimize it using time series analysis.

2. Expand the spatially explicit model of *I. typographus* to model the interaction dynamics of native and introduced bark beetles.

3. Explore the dynamics of the spatial interaction model.

The immediate outcome of our research will suggest possible changes in importation routines of wood and help forest managers to reduce the risk of spread and establishment of new bark beetles. For example, knowing the speed and pattern of spread will be important for deciding how quickly efforts should be put into action, and how large geographical areas should be involved in management plans to stop or slow down the spread of the invader. A deep understanding of the dynamics will also be useful to instruct forest industries how the risk of introductions and establishment can be minimized by changes of the importation routines. We will assess invasion risk and evaluate forest management strategies on the basis of mechanisms and observed patterns in the competition model, in particular with respect to timber import routines and scales of management. These recommendations will follow directly from the studies of spatial invasion dynamics described above. Examples of questions we will address are: how quickly does invasion propagate in space depending on species and environmental characteristics? What is the spatiotemporal distribution of outbreak patterns with the new species present? What are the relevant scales for control efforts? What are the most effective measures to prevent introduction and slow the spread?

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