

Timber import and the risk of forest pest introductions

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Summary

1. Many invasive species are introduced by trade, and there is a need for studies of pre-emptive measures to lower the risk of introductions, as post-establishment management is often extremely costly or nearly impossible.
2. In this study, we present a generic model for the first step of the invasion process for trade-imported pests, and further develop this model for potentially harmful bark beetles to assess the risk of introductions and alternative management options.
3. Our results suggest that introductions of bark beetles are likely, given present timber import practices, and that immigration may often go undetected by pheromone traps.
4. The most effective measures for reducing introduction risk were those aimed at isolating the storage from forest (storage enclosure, location) followed by those reducing the available resources for forest pests (debarking, timber irrigation, rapid processing), whereas delayed import was least effective.
5. *Synthesis and applications:* The generic model framework of species introductions presented here may easily be adapted to other import systems. The submodels of population dynamics and dispersal are also quite general, and we expect our qualitative results to hold in many cases, although the models were parameterized for bark beetles in this study. Our results suggest that detection of dispersal from storage to forests will be difficult, which implies that management actions should not be deferred until after detection in nature, as the pest species may then already be established and eradication may be too late. However, pre-emptive measures reducing propagule pressure at one or several stages of the introduction process, in particular isolation measures, may strongly reduce introduction risk.

Key-words: bark beetles, biological invasions, dispersal, forest pests, Gompertz model, *Ips* sp., pest risk assessment, propagule pressure, timber import, trade.

Introduction

With increasing global trade, there has been an upsurge in the introduction of alien species to countries worldwide (Perrings *et al.* 2005). Introduced species have caused enormous damage, and in many cases, the damage is greater in the introduced range than in the native range of the pest (e.g. gypsy moth *Lymantria dispar* in North America and *Dendroctonus valens* in China; Yan *et al.* 2005; Johnson, Liebhold & Bjørnstad 2006). This has spurred both basic and applied research on biological invasions (Hulme 2006; Liebhold & Tobin 2008). A number of models of invasions have been developed, mainly focusing on the invasion process after initial introduction, that is, population establishment and spread (e.g. Shigesada & Kawasaki 1997; Jongejans, Skarpaas & Shea 2008; Liebhold & Tobin 2008). However, in

many cases, the critical phase is the initial introduction where the alien species has yet to be introduced to natural habitats, and invasion may still be prevented by pre-emptive measures. Prevention measures are already known to be cost-effective (e.g. Richmond & Nijholt 1972; Regnander 1976; Ray & Deomano 2007), but a generic model can help evaluate the relative importance of such measures in a common setting.

In this study, we present a general model framework for the process whereby an alien organism is introduced through trade. The spread of organisms by international trade may be considered a stratified process (Shigesada & Kawasaki 1997; Hulme *et al.* 2008; Liebhold & Tobin 2008) consisting of both long and short-distance dispersal events that are caused by completely different mechanisms (e.g. international ship transport versus local transport and storage). We present a general model which captures the typical dichotomy of introduction by long-distance transport followed by local dispersal. We further refine and apply this model to assess the risk of introductions of forest pests through timber import.

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Bark beetles are major economic pests of production forests. Many potentially harmful bark beetle species are frequently intercepted around the world (Haack 2001; Brockerhoff *et al.* 2006). The small spruce bark beetle *Ips amitinus* (Eichhoff), one of the species intercepted in Scandinavia (Thunes 2003; Å. Lindelöw, personal communication), has also been caught in pheromone traps after hibernating at a Norwegian timber storage site (Økland, Kvamme & Wollebæk 2005). This raises several questions regarding the likelihood of introduction and establishment of new bark beetle species in general. It is important to evaluate the consequences of importing new beetle species, even those not known as pests in their native range since they may become primary pests when introduced to other regions (Smith & Hurley 2000).

The establishment of some bark beetle species seems to be influenced by Allee effects, since they fail to become established despite frequent interceptions (Haack 2001; Brockerhoff *et al.* 2006). The cooperative feeding behaviours of bark beetles is one potential source of such an Allee effect (Liebhold & Tobin 2008). Although Allee effects may reduce the establishment success of bark beetles, a worldwide study showed that establishment of alien bark beetles does occur, and that frequently intercepted species were about four times as likely as rarely intercepted species to become established (Brockerhoff *et al.* 2006). Thus, presumably an effective pre-emptive measure is to reduce the propagule pressure. This can be achieved in different ways at different stages during the import process.

Using the general introduction model framework presented below, we consider the different management options in the timber import system by manipulating relevant model parameters to investigate the effect on the risk of insect introductions to the forest. This is an important first step in pest risk assessment and management for these species.

Methods

We begin by developing a general import model. We then describe models and analysis for bark beetles, including the analysis of management options to reduce introduction risk. The models are parameterized from existing knowledge of the dynamics of a native bark beetle, the European spruce bark beetle *Ips typographus*. This species represents one of the most harmful forest pests in Europe (Grégoire & Evans 2004), and although native, may be a suitable organism upon which to base a worst-case scenario of introducing a new bark beetle pest. Furthermore, our model is directly relevant to areas where *I. typographus* is a potential threat, such as North America and New Zealand (Haack 2001; Brockerhoff *et al.* 2006).

A GENERAL IMPORT PROCESS MODEL

The starting point for our introduction model is the import of goods that may carry pest organisms. In general, imported goods are stored for some time before sale or processing. Import timber (the example considered below) is usually stored at open-air storage sites for a few months before processing. Although organisms can escape in small numbers at various stages of the import process (e.g. during transport

and at transportation hubs such as harbours), the storage sites are particularly important. For instance, at timber import storage sites, large amounts of timber are stored for long periods of time, enabling many organisms in the timber to complete their life cycle and disperse (Økland *et al.* 2005). Similar practices are also found in other introduction pathways, such as import of pallets, packing material, etc. Thus, our system consists of a model for local population dynamics at the storage site, and a model for dispersal to suitable habitats. The population size S_t at the storage site at the end of year t is

$$S_t = g(S_{t-1})S_{t-1} + I_t(V_t) - E_t, \quad \text{eqn 1}$$

where $g(S_{t-1})$ is the population growth rate, $I_t(V_t)$ is the import propagule pressure (the number of introduced individuals as a function of the import volume V_t), and E_t is emigration (the number of individuals escaping) from the storage site. The next step in the colonization process, immigration to natural habitats, is quantified as the number of individuals N_t reaching suitable habitat, and thus potentially founding an invader population if establishment thresholds (Allee effects) are overcome. N_t is a function of the population at the storage and the distance d between the storage and the suitable habitat:

$$N_t = f(S_t, d). \quad \text{eqn 2}$$

In this model system, several variables are relevant to management, such as the import volume and the distance or isolation between storage sites and suitable habitat. The effects of manipulating these variables depend on the structure and shape of the functions f and g . These may vary substantially among species depending on, for instance, intrinsic growth rates, the strength of density dependence and dispersal ability. In the following, we develop models (1) and (2) further for bark beetles, for which a rich literature facilitates model specification and parameterization.

MODELS AND ANALYSIS FOR BARK BEETLES

Local population dynamics

For the dynamics of bark beetles during the import process, we use an existing resource-based Gompertz model of bark beetle dynamics that agrees well with empirical time series and historical outbreak periods of *I. typographus* (Økland & Berryman 2004; Økland & Bjørnstad 2006). The growth rate of this model is

$$g(S_{t-1}) = \exp[a - a \log(S_{t-1})/\log(K_t)], \quad \text{eqn 3}$$

where S_t is the population density and K_t is the carrying capacity of the local population in year t , and a is the Gompertz growth rate. In the forest, the carrying capacity is the sum of two components formed by available windthrown trees and standing susceptible trees (see Økland & Bjørnstad 2006 for further details). At the storage site, the only resource is the stored timber, and the storage site carrying capacity is

$$K_t = \max(b_w - b_v, 2)V_t, \quad \text{eqn 4}$$

where b_w is the number of beetles produced per m^3 of timber, b_v is the number of beetles per m^3 following the imported timber from its origin, and V_t is the volume of available imported timber at the storage. By available timber, we mean the timber that is not processed before adult beetles emerge from the timber, and thus is available for

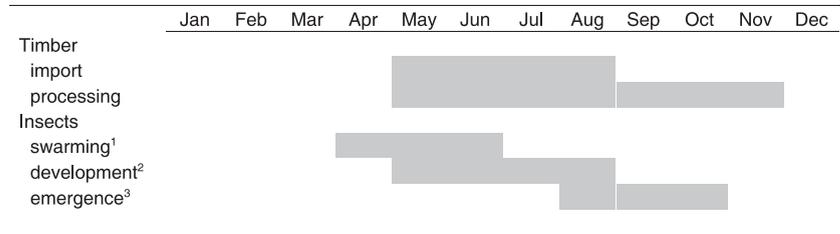


Fig. 1. Timeline of events in the timber import process and insect life histories. The figure is based on the literature for *Ips typographus* (see footnotes), but many *Ips* species and other pest insects in Scandinavian forests show similar patterns (Bakke 1961).

¹ Swarming of overwintering beetles after emergence from ground (Anonymous 1997)
² Development of new generation from egg to adult via larval and pupal stages, data for *Ips typographus* (Austarå, Midtgaard & Sæther 1993)
³ Emergence of the new generation from attacked timber, data for *Ips typographus* (Austarå, Midtgaard & Sæther 1993)

the beetles to complete their life cycle (Fig. 1). *K* is set to a minimum of two beetles per cubic metre volume, because the Gompertz population growth rate (equation 3) is not defined for $K \leq 1$. This is also biologically reasonable: regardless of timber condition and management actions (see Risk reduction analysis and Discussion), it will always be possible for beetles to exploit a small fraction of the timber.

Dispersal

The movement mechanisms of bark beetles are complex. Adult bark beetles in Scandinavia often hibernate underground, usually within a few metres from where they emerged from timber (Botterweg 1982; Austarå, Midtgaard & Sæther 1993). The main dispersal occurs during swarming in the spring, when the beetles emerge from the ground (Botterweg 1982). During outbreaks, beetles are attracted to outbreak sites (trees) by pheromones. The attraction of bark beetles to pheromone sources has been modelled using various diffusion models with drift (Helland, Anderbrant & Hoff 1989). However, most of the time, including the initial introduction phase considered here, population densities are relatively low and strong sources of attracting pheromones are few and far apart. Under such conditions, bark beetles may disperse considerable distances before encountering and reacting to attractants (Botterweg 1982; Weslien & Lindelöw 1990; Turchin & Thoeny 1993; Franklin, Debruyne & Gregoire 2000), and hence, the drift is insignificant compared to the overall dispersal distances.

To keep the model as simple as possible, we assume that the beetles move according to a simple diffusion process without drift, and that the timber storage is a point source, that is, a circular site with a relatively small radius compared to the potential extreme dispersal distances. Then, the expected number of beetles *C*(*r*) caught in a trap at distance *r* from the source can be approximated as (Turchin & Thoeny 1993, equation 6)

$$C(r) = Ar^{-\frac{1}{2}} \exp(-r/B), \tag{eqn 5}$$

where the scale parameter *A* is proportional to the product of the number of beetles released and the recapture efficiency, and the parameter *B* is proportional to the square root of the diffusion rate. The probability density of dispersal distances *k*(*r*) derived from the same diffusion model is (Turchin & Thoeny 1993, equation 9):

$$k(r) = \frac{r^{-\frac{1}{2}} \exp(-r/B)}{\int_0^{\infty} r^{-\frac{1}{2}} \exp(-r/B) dr} \tag{eqn 6}$$

Thus, the parameter *B* completely specifies the distribution of dispersal distances. The fraction of beetles dispersing a distance *d* or further from the centre of the storage is

$$m(d) = \int_d^{\infty} k(r) dr. \tag{eqn 7}$$

B was estimated by fitting equation 5 to data from three dispersal experiments by Botterweg (1982). In each of these experiments, a large number of beetles (up to 7000) were released at a central release point and trapped in annuli of pheromone traps at increasing distances (0.05, 0.10, 0.20, 0.35, 0.50 and 0.75 km) from the source. We fitted equation 5 to the mean number of beetles per trap at each distance (Botterweg 1982, Figure 7) using maximum likelihood (see e.g. Skarpaas, Shea & Bullock 2005). We only used data from Experiments 1 and 3, as these cover the range of observed dispersal distribution (in terms of long- vs. short-distance dispersal), and Experiment 2 had fewer recaptures (Botterweg 1982, Table 4).

Introduction risk: combining import, population dynamics and dispersal

To assess invasion risk, we combine the models of local population dynamics, dispersal and timber import. The import source strength, i.e. the number of beetles imported in timber with bark per year, is

$$I_t = b_v V_t, \tag{eqn 8}$$

where *b_v* is the number of beetles per m³ following the imported timber from its origin, and *V_t* is the volume of available imported timber at the storage, as described above. The number of beetles emigrating from storage is given by

$$E_t = m(d_s)[g(S_{t-1})S_{t-1} + I_t], \tag{eqn 9}$$

where *d_s* is the distance from the centre to the edge of the storage site. Immigration to natural habitats, that is, the number of beetles arriving in the forest, is

$$F_t = m(d_s + d_f)[g(S_{t-1})S_{t-1} + I_t], \tag{eqn 10}$$

where *d_f* is the distance from the edge of the storage to the edge of the forest. The number of beetles required to establish a new population depends on several factors, such as habitat structure and permanence (Paradis 1998). To provide a conservative guideline,

Table 1. Management actions to reduce introduction risk of forest pests from timber import, their effects on the system, and the equivalent model implementation. Please see the text for parameter definitions

Management action	Effect	Parameter
Import less timber	Less import volume with forest pests	Reduce V
Process timber sooner	Less time for pests to develop at storage	Reduce V
Irrigate timber	Reduce survival of pests in stored timber	Reduce V
Debark timber at source	Fewer pest individuals per import volume	Reduce b_v
Import timber later	Less time for storage population to exploit timber	Reduce b_w
Store timber far from forest	Fewer pest individuals arrive in forest	Increase d_F
Store timber in building	Fewer pest individuals escape storage	Increase d_S

we quantify invasion risk by comparing the model predictions to the abundance level needed for colonization/damage of susceptible trees, and to levels considered as outbreak conditions in established populations of *I. typographus* (Weslien *et al.* 1989; Lindelöw & Schroeder 2000). These abundances are given as counts of beetles in standard pheromone traps. We therefore convert immigrating beetle densities to trap catches using the effective attraction radius (R_{EA}) of these traps. The effective attraction radius of a trap is the radius within which all beetles are assumed to be trapped, that is, the radius of an equally effective passive trap in the same location (Byers, Anderbrant & Löfquist 1989; Schlyter 1992). We used $R_{EA} = 0.00138$ km (i.e. 1.38 m). This value was obtained for a standard *I. typographus* pipe trap (Schlyter 1992), and was intermediate for a range of pheromone traps for this species (0.0003–0.0027 km). Note that by definition, R_{EA} is much smaller than alternative measures of trap attraction, such as the sampling range or attraction range (e.g. Schlyter 1992, Figure 1), which are harder to measure and less clearly related to beetle densities in the field, and therefore less useful for our purpose.

Assuming isotropic dispersal from the storage, the expected number of beetles caught in a trap at the forest edge is

$$N_i = \frac{k(d_S + d_F)R_{EA}^2}{2(d_S + d_F)} [g(S_{i-1})S_{i-1} + I_i]. \quad \text{eqn 11}$$

While F_i gives an estimate of immigration to the surrounding forest, N_i gives a more direct measure of immediate invasion risk, as it can be compared to empirically established levels for damage to living trees or severe bark beetle outbreaks (Weslien *et al.* 1989; Lindelöw & Schroeder 2000). Both of these quantities are relevant when considering measures to reduce the risk of introductions.

Risk reduction analysis

To assess the risk of beetle introductions through timber import, we studied the sensitivity of F and N (equation 11) to model parameters and variables reflecting alternative management strategies aimed at reducing introduction risk (Table 1). These management actions affect partly separate and partly overlapping elements of the system. While de-barking will lead to a reduction in the density of beetles in the imported timber (b_v), delayed import will reduce the number of beetles produced per timber volume from the storage beetle population (b_w) because it is made available to a smaller fraction of the swarming beetles at the storage site (Fig. 1). By processing timber sooner (i.e. reducing the time window for beetles to emerge), avoiding the larval period of development and flight of the beetles, or irrigating the timber (to reduce the survival of developing beetles in the timber; Richmond & Nijholt 1972; Regnander 1976), one will

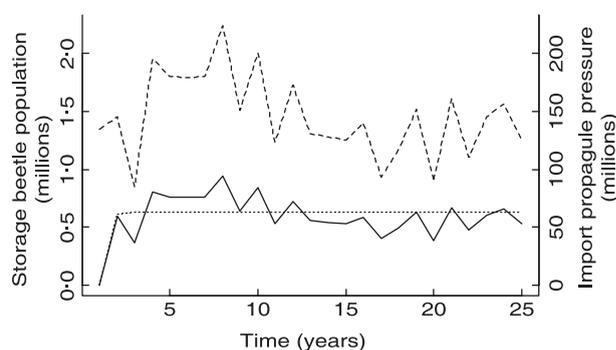


Fig. 2. Time series of simulated beetle propagule pressure through import (I_i ; dashed line, right axis) for stochastic annual variation in timber import volume ($V_i \sim$ Gaussian, mean = 150 000 m³, SD = 30 000 m³), and the corresponding population development at the storage (S_i ; solid line, left axis) with the deterministic population trajectory for constant import volume ($V = 150\,000$ m³) superimposed (dotted line). Parameter values: $a = 2$, $B = 0.46$, $d_S = 0.05$ km, $b_w = 200$ beetles m⁻³, $b_v = 163$ beetles m⁻³.

affect both the introduced beetles and the storage population. This is equivalent to reducing the volume of available import timber (V). Isolation of the storage to reduce dispersal to forest can be accomplished by locating the storage at a large distance from the forest (d_F) or by enclosing the storage. If we think of the walls of an enclosed storage building as reflecting boundaries, with the rare event of an open gate as the only escape opportunity, this is equivalent to increasing the distance from the centre to the edge of the storage site (d_S).

Realistic ranges of timber import volumes for the analyses were suggested from yearly import statistics of the local pulp industry. Parameters for the population dynamics model were obtained from the literature (see Økland & Bjørnstad 2006), and the dispersal parameters were estimated as described above. All analyses were carried out in R (R Development Core Team 2005).

Results

Starting from zero, the population of introduced beetles at the timber storage built up to a level proportional to the import source strength within a few years (Fig. 2). The storage beetle population responded to fluctuations in timber import, but for a realistic range of fluctuations in timber import, the variation in the beetle population was moderate. For a constant import rate, the storage population and the number of beetles escaping to the forest quickly reached a stable

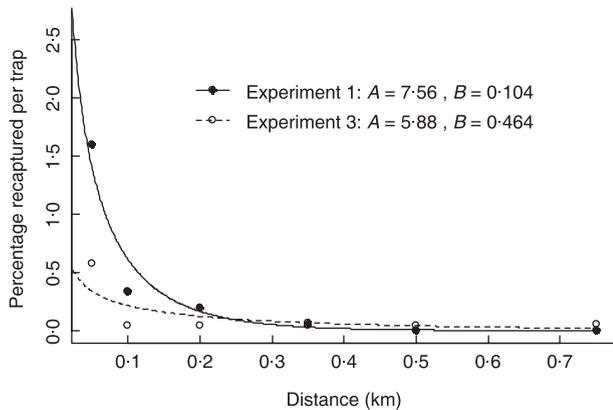


Fig. 3. Dispersal data (means of trap observations) from Botterweg's (1982) experiments 1 and 3 (points) and fitted dispersal models (equation 5; lines) with corresponding parameter estimates (A and B ; Model fit: $AIC = 20.99$ for experiment 1 and $AIC = 57.39$ for experiment 3). To make the curves comparable between experiments, Botterweg's trap count data (Botterweg 1982, Figure 7) are scaled to the number of beetles released (Botterweg 1982, Table 4) to give the percentage recapture presented here.

equilibrium depending on parameters related to import, population dynamics and dispersal.

The fitted dispersal models suggested variable patterns of dispersal for *I. typographus* (Fig. 3). The number of beetles released was lower in Botterweg's (1982) Experiment 1 (1500) than in Experiment 3 (7000), but the recapture efficiency was higher in Experiment 1 (17.8%) than in Experiment 3 (9.0%), resulting in somewhat higher estimates of A in Experiment 1 than in Experiment 3 (Fig. 3). The two experiments also differed in parameter B , which determines the shape of the dispersal curve: Experiment 3 gave a higher estimate of B , and thus, a fatter tail (more long-distance dispersal) than Experiment 1 (Fig. 3).

These differences in dispersal strongly affected the number of beetles immigrating to the forest, but did not change the relative effectiveness of alternative management actions (Fig. 4). Immigration of bark beetles to the forest was likely for wide ranges of import volumes and parameter values, and this immigration may often go undetected (Fig. 4). For high import volumes or beetle import densities, introduced beetle population densities near storage sites may even reach levels corresponding to densities observed during beetle attacks on living trees or outbreaks if the beetles are not widely dispersed (Fig. 4E–F). This is more likely for a species like *I. typographus*, which has been observed in higher densities in imported timber than for instance *I. amitinus* (mean = 163 beetles m^{-3} and SD = 77 beetles m^{-3} for *I. typographus* vs. mean = 12 beetles m^{-3} and SD = 11 beetles m^{-3} for *I. amitinus*, corresponding to annual mean import propagule pressures of about 24 and 2 million beetles, respectively; Thunes 2003; Thunes, Kvamme & Økland 2004; B. Økland, unpublished data). Introduction risk was completely insensitive to a reduction of the reproductive output of the resident storage beetle population (Fig. 4C,G). It was also relatively insensitive to changes in import volume and beetle import densities

at high levels, but more sensitive at low levels (Fig. 4A,B,E,F). However, introduction risk was quite sensitive to isolation of storage sites from suitable habitat, both to the distance between storage and forest (Fig. 4, all panels) and to efficient storage enclosures (Fig. 4D,H).

Discussion

Our results suggest that import routines strongly affect the risk of forest pest introductions. Current timber import practices are likely to lead to introductions of bark beetles, and may in some cases lead to bark beetle immigration in densities corresponding to outbreak levels at storage sites. Such high densities have been observed close to the centre of a timber storage site (Økland *et al.* 2005), but hitherto not in nearby forests.

Once alien pest species have become established in their new habitats, they may be extremely difficult to eradicate, and the costs of damage and control programmes may be high (Pimentel 2002). Despite extensive efforts in monitoring and stopping the spread of introduced species, several examples show that the range expansions continue to take place: the pine wood nematode *Bursaphelenchus xylophilus* in Portugal (Naves *et al.* 2007), gypsy moth in North America (Liebhold, Sharov & Tobin 2007), and brown spruce longhorn beetle *Tetropium fuscum* in Canada (www.inspection.gc.ca). Both theory and numerous examples show that the detection of new alien species, or localities of expansions, usually lag several years behind the actual spread of the species (Shigesada & Kawasaki 1997). Our study also suggests that immigration often may go undetected by pheromone traps (Fig. 4), implying that a monitoring system of emigration from storage sites to forests will require a high trapping intensity. Thus, investments in pre-emptive measures that will lower the risk of spread from timber storage to forests may prove to be more cost-effective than measures after new populations of alien bark beetles have established in the forest environments.

Our results suggest that the expected number of introduced beetles dispersing to the forest can be reduced effectively by increasing the isolation between storage sites and forests. The density of dispersers drops off quickly at increasing distances from the source. Although low numbers of beetles may arrive in forests far from storage sites (particularly if the dispersal capacity is high, see Figs 3 and 4), their establishment is likely to fail in the presence of Allee effects (Taylor & Hastings 2005). Therefore, a moderate increase in the distance between timber storage sites and forests may strongly reduce the likelihood of introduction and establishment. Similarly, an effective enclosure of the timber storage site will reduce introduction risk considerably. Delayed import seems to be a poor alternative. The timing of the import may also be difficult to control as the timber trade is highly dynamic in space and time (Piel *et al.* 2008). Efforts to reduce the density of beetles in imported timber (e.g. debarking) and the amount of stored timber available to the beetles (e.g. by rapid processing or irrigation of the timber)

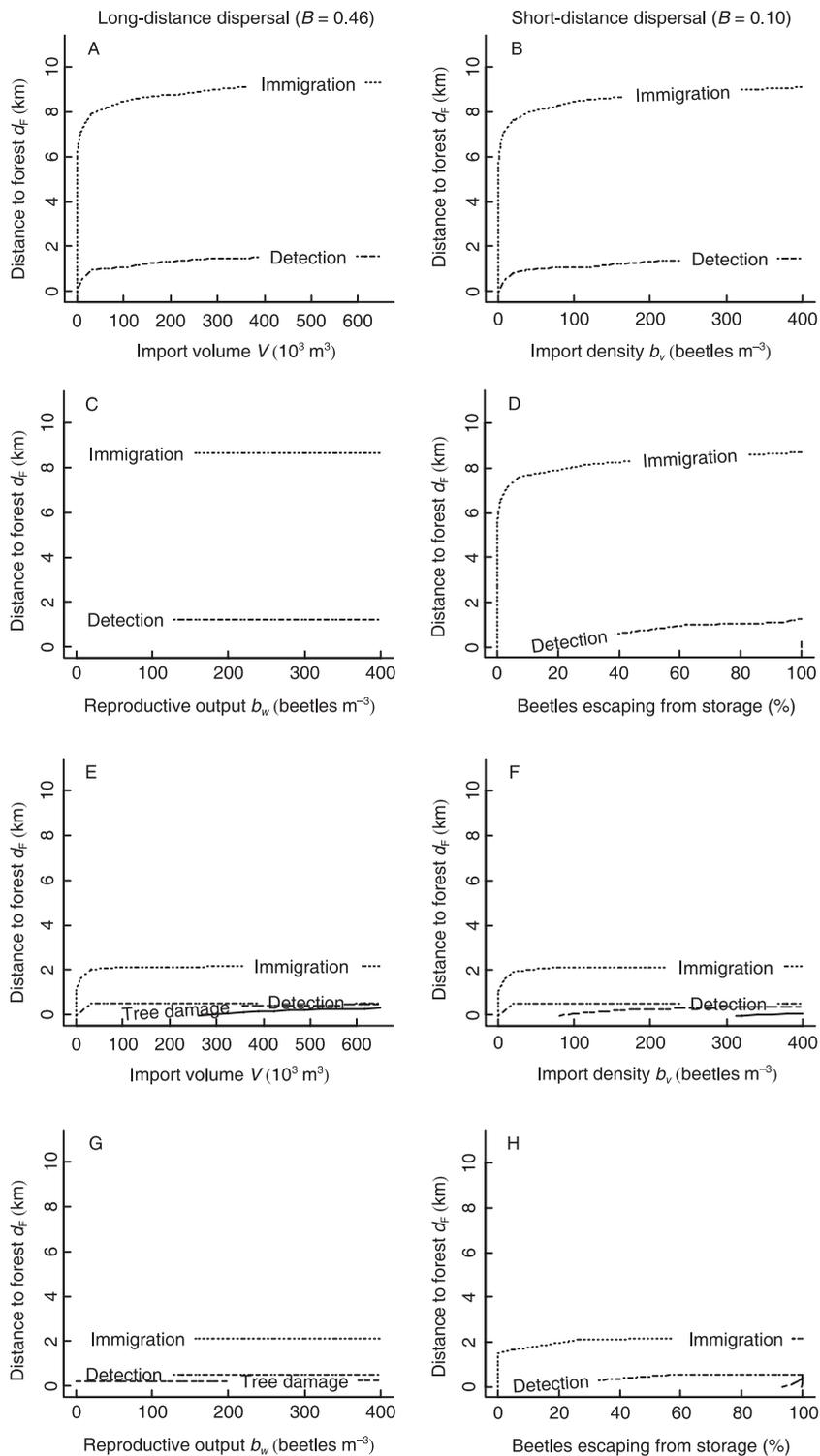


Fig. 4. Isoclines for bark beetle population densities introduced to the forest with long-distance dispersal (A–D; dispersal model as in Fig. 3, Experiment 3) and with short-distance dispersal (E–H; dispersal model as in Fig. 3, Experiment 1). The isoclines in each panel represent immigration to forest (expected number of beetles arriving in the forest $F = 1$; dotted line), detection in a single pheromone trap at the forest edge (expected number of beetles caught in a trap $N = 1$; dashed-dotted), damage to living trees ($N = 4500$; dashed), and outbreak ($N = 15\,000$; solid), as (A and E) a function of import volume (parameter values: $a = 2$, $d_s = 0.05$ km, $b_w = 200$ beetles m^{-3} , $b_v = 163$ beetles m^{-3}), (B and F) a function of beetle density in import timber (parameter values: $a = 2$, $d_s = 0.05$ km, $b_w = 200$ beetles m^{-3} , $V = 150\,000$ m^3), (C and G) a function of reproductive output (parameter values: $a = 2$, $d_s = 0.05$ km, $b_v = 163$ beetles m^{-3} , $V = 150\,000$ m^3), and (D and H) a function of storage enclosure efficiency, i.e. the proportion beetles escaping from the storage ($m(d_s)$; parameter values: $b_w = 200$ beetles m^{-3} , $b_v = 163$ beetles m^{-3} , $V = 150\,000$ m^3).

may be efficient measures if they succeed in reducing available resources or reproductive capacity considerably; the effect of such measures increase dramatically as V and b_v approach zero (Fig. 4A,B). This may be possible, but empirical studies suggest that the effects of such measures are variable. For instance, the effect of irrigation on bark beetle survival ranges from 0–20% for *I. typographus* (lower survival of larvae than pupae; Regnander 1976), 0–22% for *Pityogenes chalcographus*

(Björkhem *et al.* 1977) and 0–44% for *Trypdendron lineatum* (Richmond & Nijholt 1972). Debarking may also be effective for most subcortical insects, although some individuals in a few species may survive because they penetrate into the wood during certain life stages. Although so-called ‘bark-free’ wood often contains remains of bark (Ray & Deomano 2007), the number of individuals that survive in bark-free timber is probably low.

Thus, depending on the circumstances, single measures may have a considerable effect. Our results indicate that isolation measures may be particularly effective, whereas delayed import is least effective. However, the exact ranking of the measures will depend on the specifics of the system and the economic setting. In most cases, a combination of measures is likely to be more powerful than single measures.

Many bark beetle species have been intercepted repeatedly at harbours around the world, and many of these are potentially harmful invasives although not yet established (e.g. *I. typographus* and *Pityogenes chalcographus* in North America, *I. typographus* and *Dendroctonus ponderosae* in New Zealand and *I. amitinus* in Scandinavia; Haack 2001; Thunes 2003; Brockerhoff *et al.* 2006). Our model may be applicable in many of these cases, and our specific parameterization may be particularly useful in areas where our model species *I. typographus* is a potential invasive pest or where the species under consideration is similar (e.g. *I. amitinus*). However, by necessity, a model is a simplification of reality, based on assumptions that may or may not be fulfilled in any particular real system. To model population dynamics at the storage site, we used the Gompertz model, which seems to agree well with data for *I. typographus* in Scandinavia (Økland & Berryman 2004; Økland & Bjørnstad 2006). This model is also widely used in other systems (e.g. Edelstein-Keshet 2005). Dennis *et al.* (2006) proposed the Gompertz model as a practical general tool for modelling density dependence in the presence of observation error. They highlighted the finding by Sibly *et al.* (2005) that in 1780 time series of insects, fish, birds and mammals, the most common growth function was similar to that of the Gompertz (concave up).

The dispersal model we used is also quite general, despite the unusual dispersal characteristics of bark beetles. Bark beetle dispersal differs from the dispersal of other insects mainly in the congregation observed during mass attacks, when the beetles react to attractants released by other attacking beetles (Byers 2004). During outbreaks, bark beetle dispersal can be thought of as a diffusion process with drift towards attacked trees (e.g. Helland *et al.* 1989). However, in the present non-attacking situation, where the role of attractants is limited to the attraction radius of pheromone traps, it is reasonable to assume a general diffusion process without drift, which leads to an exponential-type model (equations 5 and 6; Turchin & Thoeny 1993). This model was originally developed for *Dendroctonus frontalis*, for which similar parameter estimates were obtained in a series of mass mark–recapture studies (Turchin & Thoeny 1993). We fitted the model to the point source mark–recapture experiments of Botterweg (1982). These experiments and the fitted models agree with other empirical studies showing that many individuals attack substrates within short distances (Wichmann & Ravn 2001), whereas some (and sometimes many) individuals may disperse long distances (Nilssen 1978; Stenseth 1984; Piel *et al.* 2005). In some cases, one may expect dispersal patterns that deviate from the exponential point source model. The assumption that the storage site is a point source for dispersal may lead to underestimation of dispersal near

the storage, but this effect is reduced at increasing distances. Conversely, density-dependent attraction may lead to lower dispersal than predicted by our model, particularly for high beetle densities. Also, the dispersal parameter surely differs among bark beetle species (Byers 2004). The model may be further developed by taking into account the influence of various environmental factors (e.g. Franklin, Debryne & Grégoire 2000; Gilbert & Grégoire 2003; Økland & Bjørnstad 2003) or the role of previous attacks (Gilbert, Vouland & Grégoire 2001) in cases where such information is available. However, the simple model used here displays the general feature of strong leptokurtosis (i.e. most individuals disperse short distances, while some disperse very far) shared by most empirically observed dispersal kernels of different insect species (Turchin 1998; Clobert *et al.* 2001; Bullock, Kenward & Hails 2002). Thus, while we cannot exclude even more long-distance dispersal in some cases, the qualitative aspects of our results are likely to hold for a range of realistic dispersal patterns.

The relationship between the number of individuals initially introduced and the long-term probability of establishment of a species is usually non-linear (Lockwood, Cassey & Blackburn 2005; Taylor & Hastings 2005). Thus, while the present analysis suggests that beetles are likely to be introduced to the forest, the establishment and spread of new populations do not automatically follow. For instance, *I. amitinus* is found in the Baltic states, Russia and Finland, and it has been observed in imported timber at harbours in USA, New Zealand, Sweden, and Norway, but not in the forests of these countries (Lindelöw 2000; Økland *et al.* 2005; Brockerhoff *et al.* 2006). Similarly, *I. typographus* has been intercepted by port inspectors in the USA 286 times from 1985–2001 (Haack 2001), but has not become established in North America. This may be a detection problem; beetles may immigrate to the forests at rates lower than the detection threshold (Fig. 4), and under suitable conditions, alien bark beetles may possibly establish populations in surrounding forests at levels far below the level of damaging living trees, which implies that the difference between detection and actual establishment may be even greater than demonstrated here. However, it may also be a real limitation on the ability of the species to establish and spread because of ecological factors, stochasticity or Allee effects (Taylor & Hastings 2005; Liebhold & Tobin 2008). Regardless of such limitations on establishment, our results suggest that introductions of bark beetles are likely to happen sooner or later, given present practices of voluminous timber import without specific control measures and, as for many other species, establishment may depend on the number of arrivals (Lockwood *et al.* 2005; Brockerhoff *et al.* 2006). According to the precautionary principle, and considering the high costs of late detections, an arriving species should be considered as non-established (and thus, a potential threat) until establishment in natural habitat has been proved. The present study may serve as a basis for investigations of the potential long-term ecological and economic consequences of such introductions, as well as for evaluations of the practicality, costs and benefits of management actions.

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