

# Is Eradication of the Pinewood Nematode (*Bursaphelenchus xylophilus*) Likely? An Evaluation of Current Contingency Plans

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The pinewood nematode (PWN) is one of the worst tree-killing exotic pests in East-Asian countries. The first European record of establishment in Portugal in 1999 triggered extensive surveys and contingency plans for eradication in European countries, including immediate removal of large areas of conifer host trees. Using Norway as an example, we applied a simulation model to evaluate the chance of successful eradication of a hypothetical introduction by the current contingency plan in a northern area where wilting symptoms are not expected to occur. Despite a highly variable spread of nematode infestations in space and time, the probability of successful eradication in 20 years was consistently low (mean 0.035, SE 0.02). The low success did not change significantly by varying the biological parameters in sensitivity analyses (SA), probably due to the late detection of infestations by the survey (mean 14.3 years). SA revealed a strong influence of management parameters. However, a high probability of eradication required unrealistic measures: achieving an eradication probability of 0.99 in 20 years required 10,000 survey samples per year and a host tree removal radius of 8,000 m around each detection point.

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**KEY WORDS:** Biological invasion; forest health; pine wilt disease; risk management; spread latency

## 1. INTRODUCTION

Once alien pest species have become established in new habitats, they may be extremely difficult to eradicate,<sup>(1)</sup> and the costs of damage and control programs may be very high.<sup>(2,3)</sup> Despite extensive efforts in monitoring and stopping the spread of introduced species, several examples show that the

range expansions continue to take place, e.g., Gypsy Moth in North America,<sup>(4)</sup> Brown Spruce Longhorn Beetle *Tetropium fuscum* in Canada,<sup>(5,6)</sup> and the pinewood nematode (PWN) *Bursaphelenchus xylophilus* (Steiner & Buhrer, 1934) Nickle (1970) in Portugal.<sup>(7)</sup>

The PWN causes pine wilt disease (PWD), which is the most important forest pest of Japan<sup>(8)</sup> and is also a significant tree killer in other countries of introduction: China, Taiwan, and Portugal. PWN is vectored by longhorn beetles in the genus *Monochamus*.<sup>(9)</sup> The first European infestation by PWN was discovered in the Setubal area south of Lisbon in Portugal in 1999.<sup>(10)</sup> Since then, large-scale control measures have been taken in and around the infested area, the aim being to stop a further

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spread of the nematode and to finally eradicate it from the EU.<sup>(11)</sup> The measures include felling and destruction of symptomatic pines within the infested area and the establishment of a surrounding host-free buffer zone. Despite these efforts, new infestations were detected outside the demarcated area in Portugal, and also in Spain.<sup>(12)</sup> The interception of PWN in Portugal has triggered detection surveys for PWN in several other European countries,<sup>(13–15)</sup> and outlines of contingency plans prescribe strong measures of eradication if PWN should be detected in their countries.<sup>(15–18)</sup> The risk of epidemic wilting of trees caused by the nematode is strongly linked to the average summer temperature. According to the ForestETP model,<sup>(19)</sup> the presence of PWN in the Nordic countries will most often not lead to PWD due to low summer temperatures.<sup>(15)</sup> Thus, it is expected to be difficult to detect PWN in a Nordic climate.

Extensive and costly measures, including detection surveys and large-scaled clearing of potential host trees, are motivated by the possibility of stopping future damages and expenses that could exceed the costs of an early eradication. However, the probability of success is a crucial point for decisions about performing very costly eradication measures. The aim of this study is to estimate this probability under Nordic conditions. We use a simulation model approach to test one example of the draft contingency plans for PWN eradication. The results of the simulations are used to evaluate the probability of eradication of the pest by the proposed measures should PWN be detected in Norway.<sup>(16)</sup> Sensitivity analyses are used to analyze the influence of the biological parameter assumptions for the model results, and to analyze how changes in the parameters of the PWN survey and the draft contingency plan of Norway can increase the probability of successful eradication.

## 2. METHODS

### 2.1. Basic System Descriptions and Model Assumptions

In the present model, we make use of the best available information for potential *Monochamus* vectors in combination with biological and climatic information from Scandinavian forest systems (see the Appendix). Biological information for potential *Monochamus* vectors in Scandinavia and their transmission efficiency are derived from several experimental studies and the PWN surveys in Scandi-

navia<sup>(14,20–22)</sup> (see the Appendix). As a supplement, we utilize information from related *Monochamus* species and forest systems to set test ranges of sensitivity analyses. In recent years, the growing interest in PWD in Europe has accelerated research on pine wilt systems in Portugal,<sup>(23)</sup> which includes one possible host that is present in Scandinavia, *Monochamus galloprovincialis* (Olivier, 1795). Furthermore, there is an extensive literature on pine wilt systems from Japan that elucidates the patterns and mechanisms of the nematode's spread within a pine stand, dispersal of vector beetles, and spread pattern of PWD.<sup>(9)</sup>

Local and regional spread of PWN is related primarily to dispersal by insect vectors of the genus *Monochamus*.<sup>(9)</sup> The principal vector in Portugal *M. galloprovincialis* is also found in the southeastern part of Norway. However, the most widely distributed species in Norway is *Monochamus sutor* (Linnaeus, 1758), which has a univoltine life cycle in southern lowland districts of Norway.<sup>(24,25)</sup> This species is also assumed to be a suitable vector for PWN.<sup>(26)</sup> It has been demonstrated to transmit *Bursaphelenchus mucronatus*,<sup>(8)</sup> a close relative to PWN occurring in Scandinavia, to dead wood via oviposition and to fresh branches of Scots pine and Norway spruce via maturation feeding.<sup>(20,21)</sup> *B. xylophilus* appears to be a superior competitor compared to *B. mucronatus*, and it cannot be stated that *B. mucronatus* will be efficient as a factor to decrease propagation of this invasive species.<sup>(27)</sup> There is abundant supply of host trees in Norway, the most important species being Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). *P. sylvestris* belongs to the group of pines that are susceptible for PWD, while PWN can live in *P. abies* but probably without developing PWD.<sup>(26)</sup> In Scandinavia, the vector *M. sutor* can oviposit and develop in recently dead wood of both tree species, while *M. galloprovincialis* is limited to recently dead pine trees.<sup>(25,28)</sup>

The transmission of PWN between the beetle generations can either go from parents to offspring in the larval habitat in dead wood or through maturation feeding on new shoots and branches of living conifers that later die and become larval habitat of *Monochamus*.<sup>(9)</sup> The latter option is important in areas with outbreaks of PWD, while the chance of transmission of nematodes in living trees to *Monochamus* beetles is considered low in a Scandinavian forest system where temperatures usually are too low for development of PWD.<sup>(15)</sup> Bergdahl and Halik<sup>(29)</sup> found that living pines can harbor PWN infestations for at least 14 years without showing

symptoms of PWD. In temperate climates healthy trees are normally not damaged by PWN, and the maximal time for latent infections to persist in living trees is not known.<sup>(26)</sup> Application of the ForestETP-model<sup>(19)</sup> in Sweden under current climatic conditions showed that the chance of PWD is small and limited to small incidences of PWD in years when summer temperatures are higher than normal in southern Sweden.<sup>(15)</sup> As long as PWD trees are rare or absent, trees infected during maturation feeding will not be a significant breeding habitat for vector beetles. Thus, the current simulation model of initial spread is limited to transmission of PWN through the larval habitat in dead conifers, so-called saprophytic life cycle.<sup>(26)</sup> The model keeps track of the living trees infested through maturation feeding; however, it is not assumed that there will be a further spread of PWN from these trees. The chance of noninfested beetles to become infested during copulation with PWN-infested beetles<sup>(30)</sup> is set to zero as the density of infested beetles will be low in the early spread of PWN.

## 2.2. Model Description

We developed a simulation model in R<sup>(31)</sup> to estimate the probability of detection and eradication should PWN enter and spread in SE Norway. In this model we assume that import of one PWN infestation (a PWN-infested beetle, e.g., *M. galloprovincialis* or *Monochamus alternatus* (Hope, 1842), or a piece of PWN-infested dead wood) leads to PWN-infection of dead-wood objects used by the local *Monochamus* populations in the lowlands of SE Norway (*M. sutor* and *M. galloprovincialis*), which in turn starts a spread of PWN to an increasing proportion of the existing *Monochamus* population and its habitat objects. As the vector has a univoltine life cycle in the risk areas for import in SE Norway,<sup>(24)</sup> the model uses annual time steps. The model keeps track of PWN-infested objects of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). According to field and survey experiences, the main habitat for oviposition is logging residues (tops, larger branches, etc.) and dead trees when they are sun-exposed, e.g., on clear-cut areas or along forest roads and margins of clear-cut areas.<sup>(32–34)</sup> The density of suitable dead-wood objects was estimated from the PWN survey<sup>(14)</sup> and the National Forest Inventory of Norway.<sup>(35)</sup>

The dispersal of the beetles in the model is divided into two components of short and long dispersal. The high abundance of *M. sutor* in newly

burnt forests far away from source habitats for these beetles shows that many beetle individuals may undertake long-distance dispersal over several kilometers in Scandinavian forests.<sup>(32,36)</sup> Several individuals may fly short distances when suitable breeding material (newly wind-felled trees) is found within or at the edges of the same area where they have developed (typical a one- to two-year-old clear-cut area). A dispersal kernel based on a mark-recapture study is described for short-distance flight of *M. alternatus*.<sup>(37)</sup> The flight distances of this kernel (mean 14 m and maximum about 60 m) are below typical distances within Scandinavian clear-cut areas. Mean of the distance across (estimated as square root of the area) 63,525 clear-cut areas in SE Norway (Fritzøe and Løvenskiold) and mid Sweden (Dalarna and Värmland) was 157 m, and 95% of the distances were within the interval 58–437 m. However, when all suitable breeding material becomes occupied or too old, several beetles must fly long distances to the next suitable clear-cut area (a clear-cut area with fresh logging residues or newly wind-felled trees), which indicates that a significant proportion of the vector beetles fly long distances. Considering the shortest distance between clear-cut areas of suitable age for *Monochamus sutor* in SE Norway (Fritzøe and Løvenskiold) and mid Sweden (Dalarna and Värmland), the mean distance was 1,170 m, with 95% of the shortest distances being within the interval 66–5,112 m. This is about the same scale as the flight distances in the mark-recapture study of *M. alternatus* (mean 1,820 m), which was used in the long-distance part of the two-component dispersal kernel described by Takasu *et al.*<sup>(37)</sup> As mark-recapture studies are lacking for *M. sutor*, we utilized the two-component dispersal kernel described by Takasu *et al.*<sup>(37)</sup> in the present simulation model. Between dead-wood objects for breeding, each individual of vector beetles were assumed to spread isotropically with randomized direction  $\theta$  of:

$$\theta \sim \text{uniform}(0 - 2\pi). \quad (1)$$

We let the flight distance  $z$  of each individual beetle (from where it was reared and PWN-infested to where it ended up laying eggs and infesting new dead-wood objects) be randomized from a dispersal distribution kernel  $F$  corresponding to the annual mark-recapture-based dispersal functions and parameterizations described by Takasu *et al.*,<sup>(37)</sup> which includes a balance between short- and long-distance

dispersal:

$$F(z) = \sigma_L f_L + (1 - \sigma_L) f_S, \quad (2)$$

where  $f_L$  is the function of long-distance dispersal,  $f_S$  is the function of short-distance dispersal, and  $\sigma_L$  is the proportion of individuals dispersing according to the long-distance dispersal component. The long-distance dispersal component is an exponential function:

$$f_L(z) = 0.000275 \exp(-0.00055z). \quad (3)$$

Among the short-dispersing beetles ( $1 - \sigma_L$ ), a fraction  $1 - \sigma_S$  remains in the same place, while the rest  $\sigma_S$  disperses a short distance according to the following function:

$$f_S(z) = \frac{0.0358}{\Gamma(0.3915)} \exp\left[-\left(\frac{z}{35.69}\right)^{2.554}\right], \quad (4)$$

where  $\Gamma$  is the gamma function.

We assume that any differences in dispersal distributions between the Scandinavian systems (*M. sutor* and *M. galloprovincialis*) and Japanese systems (*M. alternatus*) can be captured by changing the parameter  $\sigma_L$ , i.e., the fraction of long-distance dispersal, which in large part determines the shape of the dispersal kernel.  $\sigma_L$  is set to 0.35, reflecting that a large proportion of the beetle population must fly long distances to find other suitable clear-cut areas for breeding.  $\sigma_L$  is varied in sensitivity analyses in a wide range (from 0.01 to 0.7) to explore the effect of potential differences in dispersal between *M. sutor* and *M. galloprovincialis*.

The estimates of biological parameters and the ranges of biological parameter values used in sensitivity analyses (in brackets) are presented in Table I. The biological parameter values were derived from the biological literature, recent PWN research,<sup>(23)</sup> expert opinions, data from the National Forest Inventory of Norway,<sup>(35)</sup> and the PWN survey in Norway<sup>(14)</sup> and Sweden.<sup>(22)</sup> The selected estimates were based on the species and forest systems being closest to that of the model system. Further details about the parameters and their sources are given in the Appendix.

### 2.3. The Detection Survey and Its Implementation in the Model

PWN surveys were started in the Nordic countries in the year after the first detection in Portugal (1999) and have continued up to date. The surveys in Norway and Sweden are based upon the

EC Pinewood Nematode Survey Protocol 2000 and the document Nordic Pine Wood Nematode Survey, Draft Manual 2000-02-11 by Magnusson *et al.*<sup>(38)</sup> The sampling is not dependent on visible symptoms of wilt disease, but each sample requires extraction of nematodes and nematode identification by microscopy and often PCR methods to verify the presence or absence of PWN. The sampling is stratified to risk areas, which are defined as circles of 50 km radius around a point with high risk of introductions (e.g., ports of entry). Within each circle, most samples are taken from selected types of logging residues in clear-cut areas, which is the most important breeding habitat of *Monochamus* species in Scandinavia. Among the residues, samples are taken selectively from tops and thick branches (>5 cm diameter) with signs of *Monochamus* activity (e.g., exit holes, galleries, or typical saw dust). The Swedish PWN survey yielded 3,146 samples in the period 2000–2007,<sup>(22)</sup> while the Norwegian PWN survey treated 3,165 samples in the period 2000–2006.<sup>(14)</sup> This level of about 420 samples per year (representing 0.02% of the estimated number of suitable objects with *Monochamus* marks in the total sampling area of the detection survey) was used in the simulation model. The management parameters of the model were based on the Norwegian survey, where the survey included 10 circles of 50 km radius (total area 78,540 km<sup>2</sup>) and samples from both coniferous hosts of *M. sutor*: Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst). Every year of the model simulation, 420 samples were drawn randomly from the estimated total number of objects with signs of *Monochamus* breeding within the total survey area (78,540 km<sup>2</sup>), among which the PWN-infested objects were distributed during the simulated spread. Using estimates of the number of tops and large branches per pine and spruce in different diameter classes, we deployed the statistics of the average volume of logged spruce and pine per km<sup>2</sup> per year in SE Norway to estimate the total number of suitable residual objects for *Monochamus* breeding per km<sup>2</sup>. To this number, we added the number of sun-exposed recently dead pines and spruces per km<sup>2</sup> in SE Norway (estimated by the National Forest Inventory of Norway) to get the total number of suitable objects for *Monochamus* breeding per km<sup>2</sup>. This total number was multiplied by a factor representing the fraction of suitable objects that actually show signs of *Monochamus* activity (estimated from the PWN survey data), leading to an estimate of 28.8 objects per km<sup>2</sup> (Table I). When infested objects were found by

Parameter	Expected (Range)	Explanation
<b>Management parameters</b>		
samps	3,000 (3,000–450,000)	No of samples in general survey (Magnusson <i>et al.</i> 2007)
sampo	3,000 (3,000–12,000)	No of samples per year in observation zone around detection
rade	3,000 (2,000–12,000)	Radius for removing conifer trees (m)
rado	12,000 (2,000–12,000)	Width of observation zone around eradication circle (m)
<b>Biological parameters</b>		
obj	288 (166–398)	Potential dead-wood objects for <i>Monochamus</i> per km <sup>2</sup>
use	0.10 (0.08–0.12)	Ratio of potential objects occupied by <i>Monochamus</i> per km <sup>2</sup>
obju	28.80 (13.28–47.76)	No of objects occupied by <i>Monochamus</i> per km <sup>2</sup>
Burs	0.26 (0.12–0.41)	Ratio of <i>Monochamus</i> -occupied objects becoming PWN-infested
maxd <sup>a</sup>	7.488 (1.59–19.58)	Max density of PWN-infested dead-wood objects per km <sup>2</sup>
$\sigma_L$	0.40 (0.01–0.70)	Fraction of long dispersal (Takasu <i>et al.</i> 2000)
$\sigma_S$	0.671	In fraction $1-\sigma_L$ , $\sigma_S$ disperse short, and $1-\sigma_S$ stay
fem	2 (1–3)	No females ovipositing per <i>Monochamus</i> -occupied object
f	62 (37–88)	No of female eggs laid per female <i>Monochamus</i> in one season
ovi	4 (3–6)	No of objects in which each female divides her eggs
fobj <sup>a</sup>	31 (6–88)	<i>Monochamus</i> eggs laid per <i>Monochamus</i> -suitable dead-wood object
transf	0.75 (0.60–0.90)	Fraction of <i>Monochamus</i> offspring from PWN-infested object being infested
surv	0.25 (0.10–0.40)	Fraction of <i>Monochamus</i> surviving from egg till successful egg-laying adults
cop	1	Infection increase due to copulation with infected individuals (1 = 0%, 2 = 100%)
transt	0.25 (0.12–0.30)	Fraction of ovipositions by PWN-infested female leading to new infested objects
fract <sup>a</sup>	0.047 (0.0072–0.108)	No of new oviposition objects infested per previously infested objects in each time step
mat <sup>a</sup>	0.25 (0.10–0.40)	No of living trees infested per PWN-infested beetle due to maturation feeding

**Table I.** Model Parameters with Expected Values and Range of Values Included in Sensitivity Analyses

<sup>a</sup>Product parameters and parameters that are independent of other parameters.

The product parameters are:

maxd = obj \* use \* Burs.

fobj = f \* fem/ovi.

fract = transf \* surv \* cop \* transt.

the detection sampling in the simulation script, measures in the contingency plan were applied around each detection point.

#### 2.4. The Contingency Plan and its Implementation in the Model

A draft contingency plan for Norway prescribes complete logging and destruction of all host conifer trees within a circle of 3 km around each detec-

tion point and an observation zone of 17 km around this circle for intensive monitoring (3,000 samples) and preemptive measures. If additional infestations are found, new circles of logging (3 km) and intensive monitoring (17 km) should be established around the new infestation points.<sup>16</sup> Similar draft plans for large-scale eradication have been developed for other Nordic countries,<sup>(15,17)</sup> and are also included by the European and Mediterranean Plant Protection Organization (EPPO) in a standard for

control of PWN in European countries where the climate would allow PWD symptoms.<sup>(18)</sup>

Similar to the Norwegian contingency plan,<sup>(16)</sup> all infections and suitable host tree objects were removed in a radius of 3 km around all detection points before next time step of the 20-year long simulation. Furthermore, an intensive sampling of 3,000 samples was implemented in a 17-km-wide zone around the circles of tree removal, using the same estimates of sampling densities described above. For each new point of detection, a new circle of tree removal was executed before the next time step of the simulation.

### 2.5. Simulation Repetitions and Statistical Treatments

Each simulation started from an entry infestation of the pinewood nematode, and was run for 20 years to record the final eradication success when applying the PWN survey<sup>(14)</sup> and the contingency plan.<sup>(16)</sup> The 20-year simulations were repeated (30 times) to calculate each probability value, and the probability value calculations were repeated (100 times) at each set of parameter values as a basis for calculations of standard error and 95% binomial confidence intervals.

We performed sensitivity analyses to see how different parameter values influence the results and main conclusions. Since the biological parameters used in the model simulation might deviate from the true values, we applied the standardized rank regression coefficients (SRRC) to determine the biological parameters with strongest influence on the probability results of the model simulations.<sup>(39)</sup> Due to the sequential order of the dispersal and infestation processes, some of the biological parameters can be expressed as products of other parameters (see list of product parameters as footnotes in Table I). To simplify and ensure independent variables in the sensitivity analyses (SRRC), the included biological parameters were limited to product parameters and parameters that are independent of other parameters (labeled<sup>a</sup> in Table I). In addition, the effect of parameter assumptions on the model result was studied by varying each parameter one-by-one. The ranges for testing the effects of these parameters in sensitivity analyses are presented in parentheses in Table I. The SRRC calculations and analyses of individual parameters were performed in the Sensitivity package of the software R.<sup>(31)</sup>

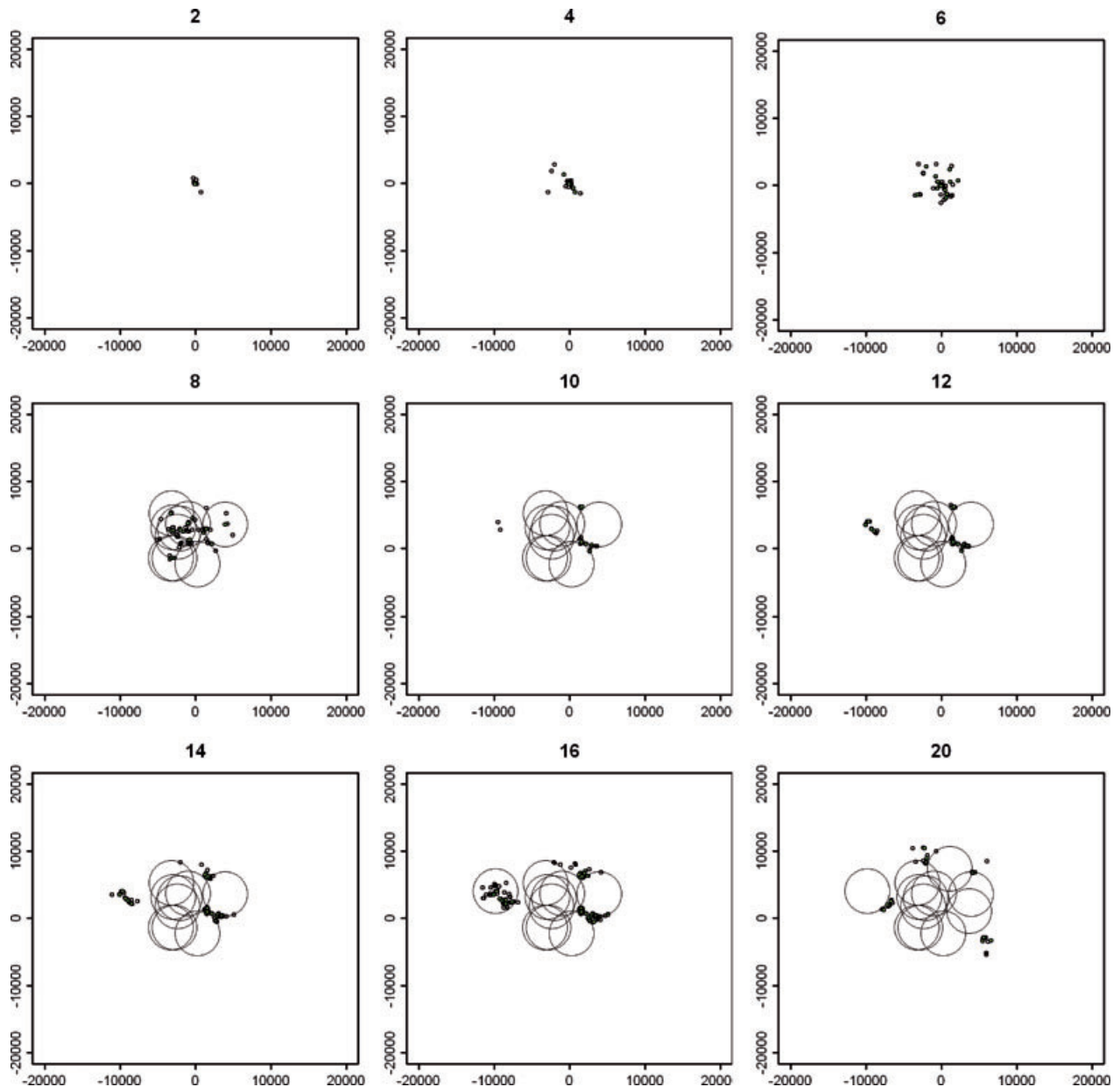
The same procedure (SRRC and varying each parameter one-by-one) was used to study the effect

of varying the management parameters on the model outcome, and to determine the levels of parameter values needed to manage with a high probability of eradication success. Using the management values with high success, a third round with the same procedure (SRRC and varying each parameter one-by-one) was used to study the influence of changing the biological parameter assumptions on the final eradication success of the model.

### 3. RESULTS

The spread of simulated nematode infestations was highly variable in space and time (Fig. 1). Due to a relatively low number of survey samples, the probability of detection in the first years was low and the spread of infestations often went undetected for several years (mean = 14.3, SE = 0.39). As the number of infestations built up exponentially, the first detection in many simulation cases consisted of several detection points. Removing the hosts trees in circles of 3 km around the detection points wiped out a large number of the infested trees; however, normally at least some infested objects, located outside the zones of eradication, were left and ensured a further spread of infestations.

The chance of successful eradication by the contingency plan appeared to be small in the current simulation results. Using the expected values of biological and management parameters, the mean probability of successful eradication was 0.035 (SE = 0.02). Due to uncertainties in parameter values, the sensitivity of the model outcome was tested in a wide range for all of the biological parameters (Table I; see also the Appendix). None of the biological variables showed any significant influence on the probability of successful eradication, neither in sensitivity analysis varying all of the biological parameters simultaneously (Fig. 2(a)), nor when each of the biological parameters were varied one-by-one. Varying each of the biological parameters *fract* (number of new oviposition objects infested per each already infested objects in each time step), *maxd* (maximal density of PWN-infested deadwood objects per km<sup>2</sup>), and *mat* (number of living trees infested per PWN-infested beetle due to maturation feeding), the probability of eradication remained constantly low in the same way as demonstrated for the parameter *fobj* (the number of *Monochamus* eggs laid per *Monochamus*-suitable dead-wood object) in Fig. 2(b). The only exception from noninfluence of the biological parameters was a slight increase of

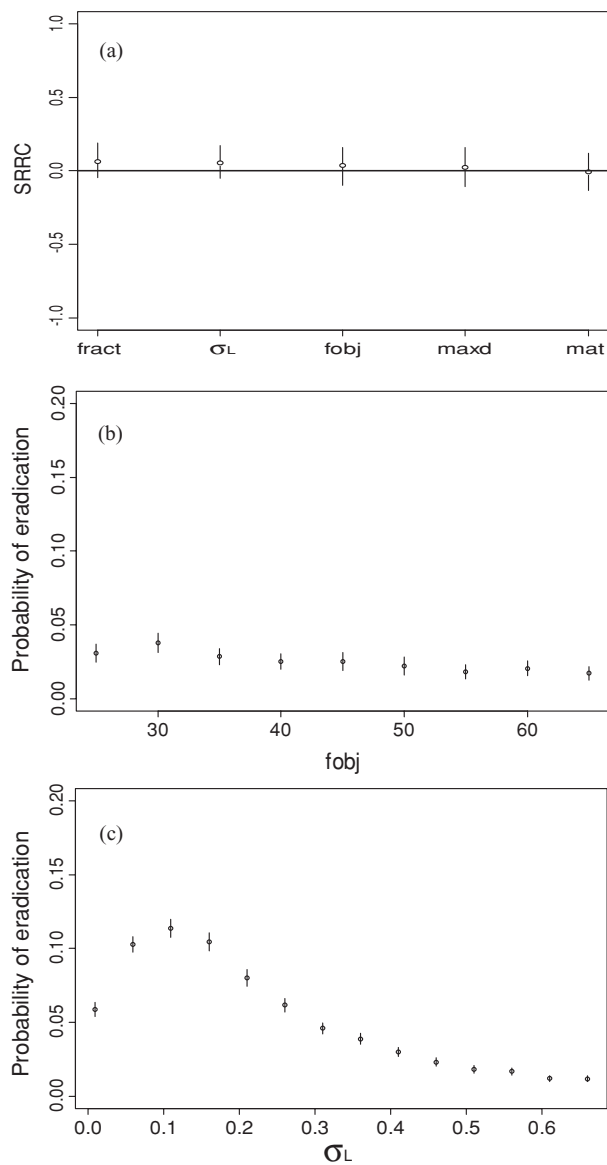


**Fig. 1.** Example of simulated spread of pinewood nematode infestations vectored by *Monochamus* beetles in conifer forest (figures for the years 2, 4, 6, 8, 10, 12, 14, 16, and 20). Small black circles = infestations of dead wood. Green points = living trees infested by maturation feeding of the beetles. Large circle = circular area of 3 km radius where all conifer trees are removed and destructed immediately after detection of infestation, in accordance with the Norwegian contingency plan. In the present example, the first detection of infestations by the survey happened in year 8, followed by removal of host trees in circles of 3 km radius around each detection point, which was nevertheless insufficient to achieve full eradication. The intensive sampling in the observation zones around circles of removal resulted in further detections and new circles of tree removal in the years 16, 17, and 19. Even though the number of infestations was reduced by removing trees, there were still infestations in year 20.

eradication probability when the dispersal capability of *Monochamus* beetles was set lower, exhibiting a maximum probability of 0.12 for  $\sigma_L$  (fraction of long dispersal) being 0.1 (Fig. 2(c)). Noteworthy, a further

decrease of  $\sigma_L$  below 0.1 resulted in lower eradication probability.

Changes in the management parameters had a strong influence on the probability of eradication.



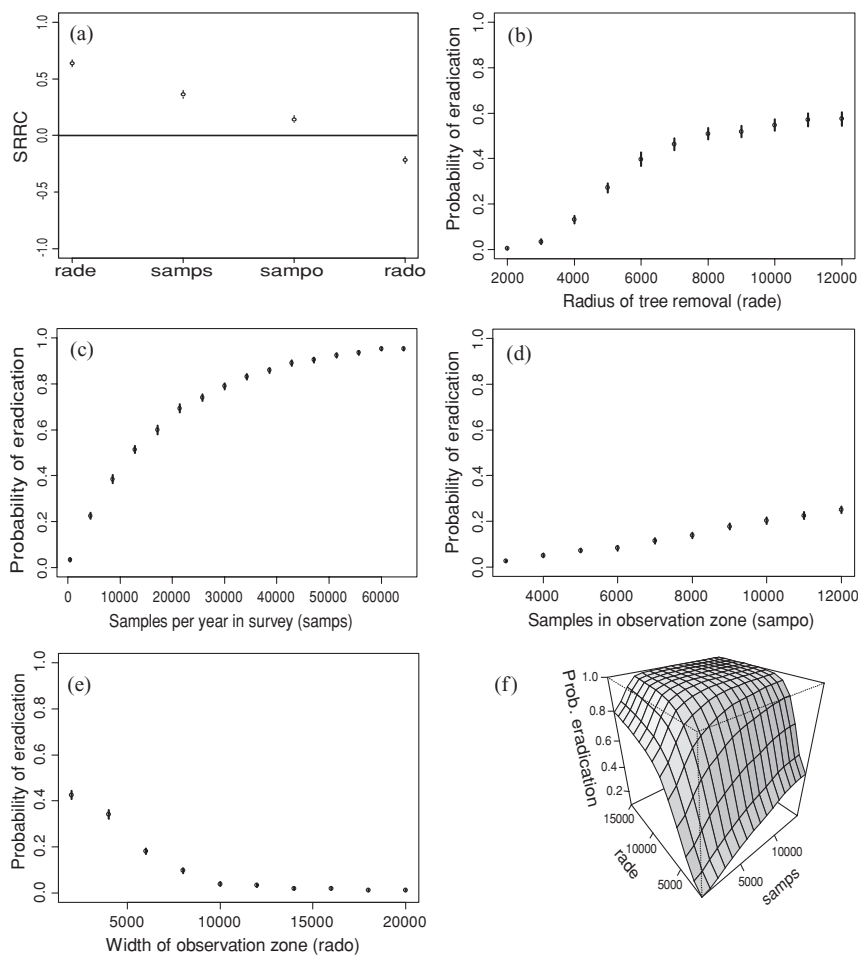
**Fig. 2.** Sensitivity analyses of biological parameters on the model outcome assuming management parameters according to the contingency plan. (a) Nonparametric sensitivity analysis (SRRC) for all biological parameters, and probability of eradication as function of each of the biological parameters, (b) *fobj* (the number of *Monochamus* eggs laid per *Monochamus*-suitable deadwood object), and (c)  $\sigma_L$  (the fraction of long dispersal). CI = 95%.

Using nonparametric sensitivity analysis (SRRC) on all management parameters, the strongest influence on the eradication probability was found for the tree removal radius around detection points (*rade*) and the number of survey samples (*samps*), while the number of samples in the observation zone (*sampo*) had only a small positive influence, and the width of

the observation zone (*rado*) had a negative impact on the model outcome (Fig. 3(a)). Varying management parameters one at a time, the probability of eradication appeared as a logistic-shaped function of the radius of removing trees (*rade*) leveling off at probability values below 0.6 (Fig. 3(b)). Varying only the number of survey samples (*samps*), a high probability of eradication (about 0.95) can be achieved when the sampling intensity is very high (above 60,000 samples per year; Fig. 3(c)). Even this large number of samples represents only 2.65% of the estimated number of suitable objects with *Monochamus* marks in the total sampling area of the detection survey. An increase in eradication probability was also found by increasing the number of samples in the observation zone (*sampo*); however, the probability was still low (0.24) for a high number of samples per year (12,000; Fig. 3(d)). In contrast, the eradication probability decreased with increasing width of the observation zone (*rado*), approaching very low probabilities (<0.05) for widths above 10 km (Fig. 3(e)). Fig. 3(f) presents the probability of eradication when varying the two management parameters with the strongest influence on the eradication probability. Even with this approach, very high values were required for achieving a high likelihood of eradication success. Choosing the combination of management parameters with lowest possible radius of tree removal (*rade*), a 0.99 probability of eradication success was achieved by a radius of 8,000 m for removing host trees and including 10,000 survey samples per year, while a 0.999 probability of success required a radius of 10,000 m and 11,600 samples per year. The model outcome was also insensitive to biological parameters when the management parameters were set to maximize the likelihood of eradication.

Early detection of the first infestation appears to be a key condition for successful eradication. The time until detection is a strongly declining function of the number of survey samples per year (Fig. 4(a)). With the sample intensity of the current survey (about 420 samples per year), the probability of detection within the first year is 0.00013 and within the fourth year about 0.011. Even with a large number of samples, detection during the first years is not guaranteed. For instance, with 60,000 samples per year, the probability of detecting the infestation within the first year is 0.17 and within the fourth year about 0.8 (Fig. 4(b)). The time until detection is also sensitive to the biological parameters that directly or indirectly influence the density of infestations that the general survey should sample from; however, the





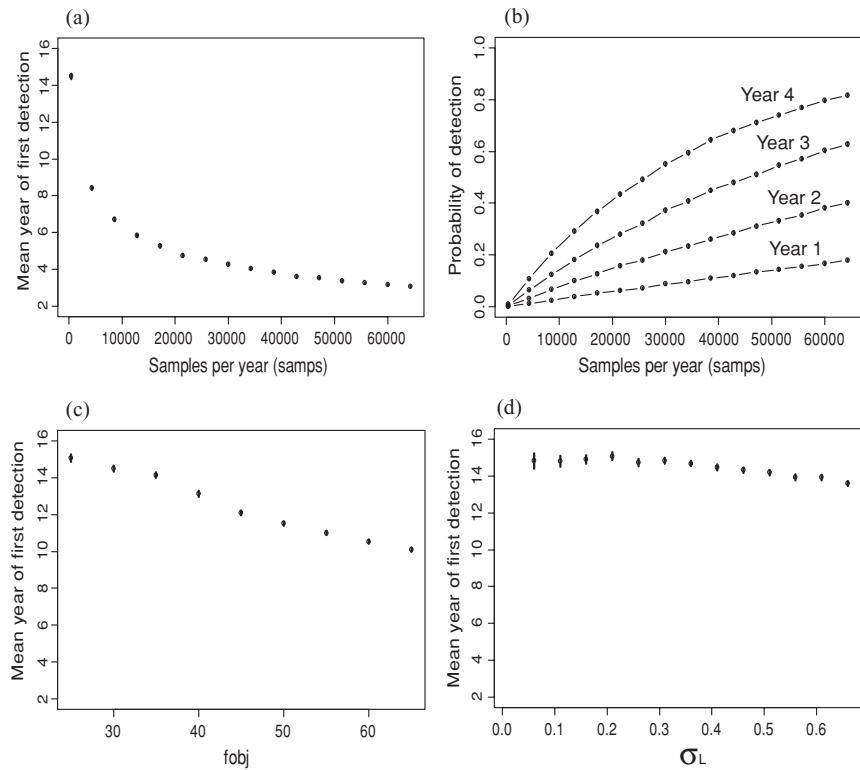
**Fig. 3.** Sensitivity analyses of management parameters, implementing all parameters in a nonparametric sensitivity analysis, SRRC (a), and varying separately each of the parameters radius of tree removal—*rade* (b), number of survey samples per year—*samps* (c), number of samples in the observation zone—*sampo* (d), and width of the observation zone—*rado* (e). Fig. 3(f) presents a biplot of the eradication probability as a function of the two parameters with strongest influence, *rade* and *samps*. Radius values of *rade* and *rado* are given in meters. CI = 95%.

influence is much smaller than for the sample intensity. The time until detection is falling with increasing values of *fobj* (the number of *Monochamus* eggs laid per *Monochamus*-suitable dead-wood object; Fig. 4(c)), *fract* (number of new oviposition objects infested per each already infested objects in each time step), *maxd* (maximal density of PWN-infested dead-wood objects per km<sup>2</sup>; both *fract* and *maxd* show near identical patterns as Fig. 4(c) in their test ranges; not presented in figure) and  $\sigma_L$  (fraction of long dispersal), except for  $\sigma_L$ -values below 0.1 where decreasing dispersal causes local distributions of infestations with low probability of detection in time before the population becomes too widespread for eradication (Fig. 4(d)).

By using the parameter values in the survey and contingency plan, the total area of tree removal after 20 years of eradication efforts is on an average 314 km<sup>2</sup> (SE = 21.1 km<sup>2</sup>). The total area is a positive function of the radius used in each circle of tree

removal (Fig. 5(a)), while increasing sampling intensity (*samps*) reduces the total area of tree removal (Fig. 5(b)). The total area of tree removal is also a positive function of biological parameters that are associated with the spatial density of infestations. In their test ranges, total area of tree removal is increasing with *fobj* (from 188 to 600 km<sup>2</sup>), *fract* (from 250 to 607 km<sup>2</sup>), *maxd* (from 33 to 364 km<sup>2</sup>), and  $\sigma_L$  (from 1.4 to 543 km<sup>2</sup>). As delayed detection and exponential spread often resulted in a large number of infestation points in the first detection, a large area of forest would have to be removed during one winter, before the insects start spreading again in the spring. There are roughly about 500 harvesters in Norway, of which each machine can fell trees in an area about 20–30 m × 100–150 m per working day (Einar Østhassel, personal communication, 2009). Thus a maximum total area of 426 km<sup>2</sup> forest can be removed by all the harvesters in the period August 1–May 1. Using the expected parameter values of the survey and the

**Fig. 4.** Parameters influencing detection time. The number of years until the first detection of infested objects when varying the number of survey samples per year—*samps* (a), the number of *Monochamus* eggs laid per *Monochamus*-suitable dead-wood object—*fobj* (c), and the fraction of long dispersal —  $\sigma_L$  (d); and the probabilities of detection within the first, second, third, and fourth years when varying *samps* (b). CI = 95%.

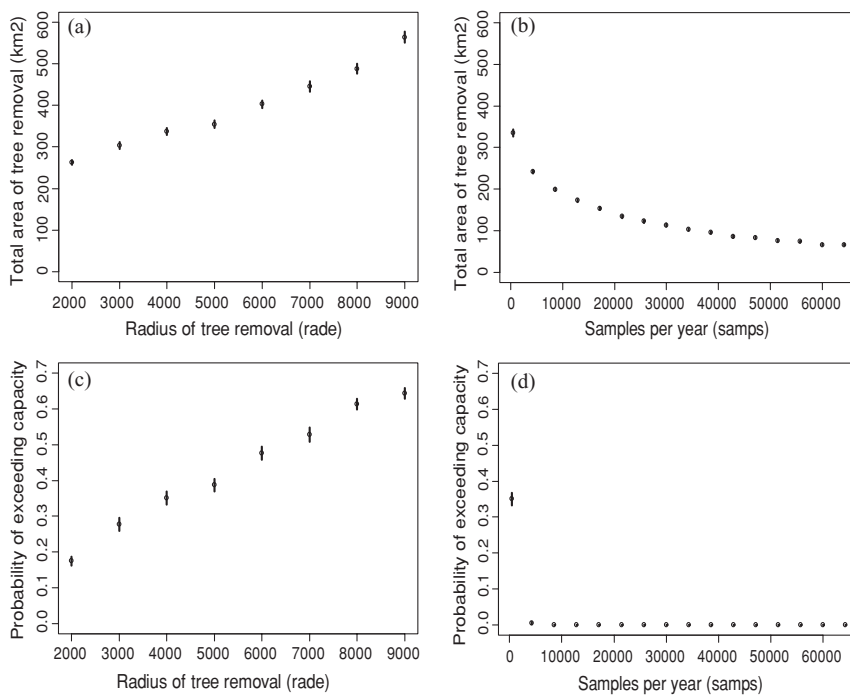


contingency plan, the probability of exceeding the logging capacity of all logging harvesters (426 km<sup>2</sup>) in the first detection of the simulations was 0.32 (SE = 0.04). The probability of exceeding this limit is an increasing function of the radius of tree removal (Fig. 5(c)) and a declining function of the number of survey samples (Fig. 5(d)).

#### 4. DISCUSSION

The prospects of extensive damage by serious pests has been used as an argument to prescribe strong eradication measures that can stop further spread from the beginning.<sup>(40)</sup> The comprehensive forest damage caused by the pinewood nematode in East Asia<sup>(8)</sup> and the entry of this pest in Portugal and Spain<sup>(10,12)</sup> has motivated the development of very demanding contingency plans in North European countries for early eradication of eventual new introductions.<sup>(15–18)</sup> All of these plans require large investments and efforts. Our simulations contribute to a critical assessment of these investments in northern areas where wilting symptoms are not expected to occur. Testing one representative contingency plan of the Nordic countries (Norway), we found that the chance of successful eradication by

the contingency plan is very low (0.035, SE = 0.02). The parameters were in a most realistic way based on empirical data and experiments. We used a dispersal kernel based on mark-recapture studies of a different species, *M. alternatus*; however, field studies in Scandinavia indicate a fraction of long dispersal in *M. sutor* that is about the same level or even higher than in *M. alternatus*. Even though the model results cannot be verified directly against data of a PWN introduction in North Europe, the result appears robust as the success remained low even when biological parameters were varied and tested in sensitivity analyses. Decreasing the only biological parameter with a response, the dispersal parameter  $\sigma_L$ , gave a minor increase of the eradication probability up to 0.12 (Fig. 2(c)); however, a further decrease of the fraction below 0.1 resulted in lower eradication probability, probably because a small density-regulated population with little dispersal tends to be difficult to detect in time by the survey. The low probability estimate is conservative due to its dependence on several ideal assumptions that tend to lower the eradication success. For instance, it does not take into account that introductions could happen outside the 10 survey areas,<sup>(14)</sup> that logging and destruction of host trees can fail to finish before the start of the



**Fig. 5.** The total area of tree removal (a, b), and the probability of exceeding the estimated total capacity of all harvesters in Norway (426 km<sup>2</sup>) in the year of first detection (c, d), when varying the radius of tree removal—*rade* (a, c) and the number of samples in the survey—*samps* (b, d). Radius values of *rade* are given in meters. CI = 95.

next flight period of the beetles and that irregularities can cause infested substrates to be overlooked, or that PWN in some cases is not found in the samples even though it is present in the sampled objects. Furthermore, the model does not take into account human-mediated dispersal, which could contribute to the spread of PWN during a period of delayed detection, although the impact of this factor is expected to be lower in sparsely populated areas of Northern Europe.<sup>(41)</sup>

Delayed detection seems to be a major factor for the low success of eradication. Most often there is a time lag between the initial arrival and when the established populations are noticed. Even when an invasive species creates visible symptoms, the delay may be a result of the time needed for population growth of populations from founding levels to densities sufficient such that they might be detected. Detection delays are indicated by both theoretical studies and empirical studies.<sup>(42,43)</sup> For instance, a delay of approximately 12 years is reported for detecting the presence of the gypsy moth in North America,<sup>(43)</sup> and at least nine years for *Dendroctonus micans* in the United Kingdom.<sup>(44,45)</sup> The delay in detection of a potential pinewood nematode introduction in northern Europe may be even longer, as symptoms are assumed to be absent at northern latitudes<sup>(15)</sup> and detection depends on resource-demanding sampling and lab-

oratory analyses. Assuming the sampling density of the current detection survey in Norway,<sup>(14)</sup> our simulation results showed an average of about 14 years until the first detection of infested objects. This long delay is also a plausible explanation for the lack of sensitivity to biological parameters, and the limited influence of other management parameters.

It seems difficult to achieve a high success of eradication by adjusting the parameters involved in the contingency plan. One parameter, the width of the observation zone (*rado*), even had a negative impact on the eradication success due to its diluting effect on the sampling. Improving one of the best parameter candidates from the sensitivity analyses, the success by increasing the circle of tree removal, did not exceed about 60% even for very large circles (Fig. 3(b)), while an unrealistically high number of samples (60,000 samples per year) was required to achieve 95% eradication success (Fig. 3(c)). As demonstrated by Bogich *et al.*<sup>(46)</sup> management programmes should consider the combination of both monitoring and eradication efforts. We searched for the combination of monitoring and eradication intensities with lowest cost (lowest radius of tree removal, assuming that tree removal is more costly than survey sample analyses) that could satisfy a high eradication success (99 or 99.9%). However, even when both the number of survey samples and the radius of removing host trees were increased simultaneously,

a sufficient eradication success demanded unrealistically high levels of survey sampling and forest clearing. A 99% chance of successful eradication required 10,000 samples per year and removal of trees in a radius of 8,000 m (201 km<sup>2</sup>), while 99.9% chance of success required 11,600 samples per year and a radius of 10,000 m (314 km<sup>2</sup>) (Fig. 3(f)). According to statistics of the National Forest Inventory of Norway,<sup>(47)</sup> a circular area of radius 8 km in the forest of SE Norway contains about 20 million trees, and with radius 10 km the tree number is above 30 million. In this success estimate, it is assumed that the large number of samples cover all 10 circular areas of 50 km radius<sup>(14)</sup> and are completed every year, and with enough time for a complete logging and destruction of the large number of trees before the next flight season if infestations should be detected. In addition, more than one infestation may be detected, which may imply removal and destruction of trees over very large areas (Fig. 5). When several infestations are detected in the same year, the total area for tree removal may override any realistic level of what can be logged by the total capacity of harvesters in Norway. In additions to the economic costs associated with the large-scale sampling and logging, such levels of clear-cutting will also dramatically affect the quality of the forests in several respects (biodiversity, recreation, hunting, etc.).

It is important to distinguish between spread of PWN and expansion of their symptoms of wilting and tree-killing (PWD). The model study of spread in China was based on verifications against killed trees and areal distributions given by observation of wilt symptoms, and did not take into account the latent infestations of PWN.<sup>(41)</sup> The spread of PWD appears to be limited by an Allee threshold in density of wide-traveling individuals that are needed to create symptoms, which in turn may be influenced by the build-up of high populations in core areas from where the nematode-infested beetles are spreading.<sup>(41)</sup> A similar Allee threshold can also be found for the spread of PWN if the production of vector beetles is dependent on the breeding habitats created by PWD and no or little other dead wood habitats are found for the vectors production; however, verification of this cannot be done without data on the distribution of latent infections. According to the model of Yoshimura *et al.*<sup>(48)</sup> where the “basic reproductive rate” of the vector beetles depends on the density of pines killed by the pinewood nematodes, the spread of the pinewood nematodes fails when the beetle density is below a certain threshold. This

type of Allee effect is unlikely to limit the spread of an eventual PWN infestation in Scandinavia, where the nematodes are assumed to spread efficiently by beetles<sup>(49)</sup> in already existing and widely distributed *Monochamus* populations,<sup>(28,32)</sup> and independently of pine killing as these beetles breed and transfer nematodes mainly in the resources of fresh dead wood created abundantly by the logging practice in this region.<sup>(14)</sup> If an infestation is detected in Scandinavian forests, it can be assumed that the transmission and spreading process is successful and that the infestation is already widespread, unless specific information shows a short time lag since entry of the pest.

Still, an Allee effect may open interesting perspectives for management of eventual PWN infestations in Northern Europe where the pest cannot be tracked by wilting symptoms. Creating an Allee effect due to beetle density may be a way to control and slow the further spread of PWN when infestations are detected after being spread over a wide area and no wilting symptoms can be observed. Reducing the abundance of suitable breeding substrates for the vector beetles (logged tops, sun-exposed dead wood, etc.) may slow the further spread and lower the populations in the infested area to a level where stochastic processes might eradicate PWN.<sup>(50)</sup> Removal of logging residues is much cheaper and more feasible than large-scale clear-cutting; however, the possible gains should be compared to the negative effects on biodiversity. Our simulations showed that the areal extent and the maximal distances of the infestations were reduced with decrease in parameters associated with breeding substrate density and offspring productivity. These results are also consistent with studies where the availability of vectors may be dependent on PWD,<sup>(37,41,48)</sup> and general theoretical studies showing that spread rates and distances are positive functions of the growth rate of the organisms.<sup>(42,51,52)</sup>

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#### APPENDIX: SOURCES FOR PARAMETER ESTIMATES AND RANGES

*samps*: 3,165 samples in Norway in the period 2000–2006,<sup>(14)</sup> 3,146 samples in Sweden in the period 2000–2007.<sup>(22)</sup>

*sampo*: 3,000 samples in the observation zone.<sup>(16)</sup>

*rade*: a radius of 3,000 m for destruction of all coniferous host trees.<sup>(16)</sup>

*rado*: radius of 17,000 m for the observation zone,<sup>(16)</sup> later adjusted to 12,000 m (Christer Magnusson, personal communication, 2009).

*obj*: 288 potential deadwood objects for *Monochamus* per km<sup>2</sup> is based on empirical data for branch sizes of various diameter classes of *Picea abies* and *Pinus sylvestris* trees (Norwegian Forest and Landscape Institute), logging statistics of Norway and other forest structure data from Statistics Norway ([www.ssb.no](http://www.ssb.no)) and the National Forest Inventory of Norway ([www.skogoglandskap.no](http://www.skogoglandskap.no)). We used estimates of the number of tops and large branches (>5 cm diameter) per pine and spruce in different diameter classes. From these object-diameter relationships and diameter-volume distributions of pine and spruce forests in SE Norway (estimated by the National Forest Inventory of Norway), we could estimate the average number of suitable objects of tops and large branches produced per cubic meter of clear-cut logging in SE Norway. Multiplying this number of objects per cubic meter with the average volume (cubic meter) of logged spruce and pine per km<sup>2</sup> per year in SE Norway (data from Statistics Norway, [www.ssb.no](http://www.ssb.no)), we estimated the total number of suitable residual objects for *Monochamus* breeding per km<sup>2</sup>. To this number, we added the number of sun-exposed recently dead pines and spruces per km<sup>2</sup> occurring in margins of clear-cut areas and roads in SE Norway (estimated

by the National Forest Inventory of Norway), to get the total number of suitable objects for *Monochamus* breeding per km<sup>2</sup>.

*use*: a fraction of 0.1 for the fraction of suitable objects that actually have marks of *Monochamus* activities was estimated from field data of the PWN survey.<sup>(14)</sup>

$obju = obj * use.$

*Burs*: 0.26 is found if we assume a fraction 0.24 for infested beetles of those reared out (14 of 59 *M. sutor* were infested with *B. mucronatus*)<sup>(21)</sup> and 91% risk of contamination (20 of 22 callow adults of *M. galloprovincialis* were infested with *B. xylophilus*);<sup>(23)</sup> or alternatively 0.41 as 14 of 34 *Monochamus* beetles from the province of Dalarna contained *B. mucronatus*;<sup>(49)</sup> or 0.12 as 20 of 171 *Monochamus*-samples from Snippen and Våler in Norway contained *B. mucronatus* (Christer Magnusson, pers. comm.).

$maxd = obj * use * Burs.$

$\sigma_L$  and  $\sigma_S$  are adopted from the dispersal kernel based on mark-recapture studies described by Takasu *et al.*<sup>(37)</sup>

*fem*: based on the field observation of the sample survey,<sup>(14)</sup> it is concluded that each object (most often a tree top after logging) contains one to two larvae, rarely three; and all one to three larvae in one object can be assumed to derive from offspring of the same mother.

*f*: the number 50 eggs per female *M. sutor* derives from beetles caught in the field;<sup>(32)</sup> 88 is the double of 44 eggs per *M. sutor* female during three weeks of oviposition when we assume a total oviposition period of six weeks;<sup>(20)</sup> 67 is an average of eggs laid per *M. galloprovincialis* female during 54 days,<sup>(23,53)</sup> while 37 is the number of eggs per *M. galloprovincialis* female found by Franchardi and Pennachio;<sup>(54)</sup> 45–87 eggs per *M. galloprovincialis* female derives from Hellrigl;<sup>(55)</sup> 80 is the maximum number of eggs per female *M. alternatus* derived from Togashi;<sup>(56)</sup> 86.2 is the mean egg number per *M. alternatus* female in field cage studies by Togashi and Magira.<sup>(57)</sup> While studies of *M. carolinensis* indicate a lower intrinsic rate of increase when the nematode load is high,<sup>(58)</sup> we assume that the nematode load in beginning spread of PWN after a new introduction is not high enough to be a significant factor with influence on *f*.

*ovi*: 3 is an estimate based on Hughes and Hughes.<sup>(59)</sup>

$fobj = f * fem/ovi.$

*transf*: 0.91 is given by that 20 of 22 callow adults of *M. galloprovincialis* were infested with *B. xylophilus*.<sup>(23)</sup>

*surv*: 0.05 is survival for *Monochamus scutellatus*;<sup>(60)</sup> 0.15 is a result for *M. carolinensis* and *M. titillator* not including mortality of eggs;<sup>(61,62)</sup> 0.249 is the mean survival from egg to adult emergence (range 0.129–0.298) of *M. alternatus* on *P. thunbergii*;<sup>(63)</sup> 0.289 survival rates found for *M. alternatus* in field cages;<sup>(57)</sup> 0.54 can be estimated as a product of survival for the eggs (0.84), small larvae (0.89), large larvae (0.74), pupae (0.992), and adults in pupal chambers (0.98) of *M. galloprovincialis* in a laboratory experiment where survival may be higher than in nature.<sup>(23)</sup> While studies of *M. carolinensis* indicate a lower intrinsic rate of increase when the nematode load is high,<sup>(58)</sup> we assume that the nematode load in beginning spread of PWN after a new introduction is not high enough to be a significant factor with influence on *surv*.

*cop*: set at 1; *cop* is an index value of additional nematode-free individuals of *M. alternatus* that are infected during copulation with infected individuals ( $cop = >1$ ); however, the number of transferred nematodes is low or zero ( $cop = 1$ ) when the infectors carry few nematodes.<sup>(30)</sup>

*transt*: 0.12 is derived from Schroeder and Magnusson<sup>(20)</sup> for transmission of *Bursaphelenchus mucronatus* by *M. sutor*; 0.25 was the transmission of *B. xylophilus* found for *M. carolinensis*;<sup>(64)</sup> 0.37 is given by a laboratory experiment where egg-laying by *M. galliprovincialis* infested by *B. xylophilus* resulted in infestation of 37% of the pine bolts.<sup>(7,23)</sup>

$fract = transf * surv * cop * transt$ .

*mat*: 0.14 derives from field experiment where 14% of the field trap-trees became PWN-infested after oviposition by *M. galliprovincialis*; while 0.37 was the fraction of laboratory bolts that became PWN-infested after maturation feeding by *M. galliprovincialis* in Portugal;<sup>(7,23)</sup> and in Japan each vector beetle of *M. alternatus* contributed on an average to one to two killed trees due to maturation feeding.<sup>(15)</sup>

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