

Transition from windfall- to patch-driven outbreak dynamics of the spruce bark beetle *Ips typographus*



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ARTICLE INFO

Article history:

Received 14 August 2015

Received in revised form 1 December 2015

Accepted 11 December 2015

Keywords:

Insect outbreak

European spruce bark beetle

Windthrow

Infestation spots

Spatial simulation model

Aggregation pheromone

ABSTRACT

The purpose of this study is to increase the basic understanding of outbreak dynamics in order to improve the management of bark beetle outbreaks. The spruce bark beetle *Ips typographus* is a major disturbance agent of European forests and is the continent's most economically and environmentally damaging bark beetle. Outbreaks of the spruce bark beetle are often triggered by large windfall episodes, and we have utilized a unique opportunity to study a Slovakian outbreak where little salvage logging was performed in some areas after a 2.5 million m³ storm-felling in 2004.

Our analyses focused on the first five years after the windfall, and we used a combination of empirical data and simulation models to understand the spatial patterns of beetle-killed forest patches developing during the outbreak. The univoltine beetle population used an increasing proportion of the windfelled trees during the two first seasons after the storm, but from the third season onwards our comparisons of inter-patch distance distributions indicated a transition from beetle production largely in windfall areas to a self-sustaining outbreak with infestation patches developing independently of the windthrows. The size of new infestation patches formed after this transition was modeled as a function of beetle pressure, estimated by the proportion of a circle area surrounding new patches that was covered by infestation patches the previous year. Our model results of patch size distribution did not correspond well with the empirical data if patch formation was modeled as a pure dispersal–diffusion process. However, beetle aggregation on individual trees appears to be important for patch development, since good correspondence with empirical data was found when beetle aggregation was incorporated in the modeled dispersal process. The strength of correspondence between the beetle aggregation model and the empirical data varied with the density of aggregation trees in the modeled landscape, and reached a maximum of 83% for a density of three aggregation trees per infestation patch.

Our results suggest that efficient removal of windfelled trees up until the start of the second summer after a major windfall is important to avoid a transition into a patch-driven bark beetle outbreak that is very difficult to manage. Our results also indicate that the outcome of a patch-driven outbreak is difficult to predict, since the development of new infestation patches is not a simple function of beetle pressure but is also affected by beetle behavior and local forest conditions.

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1. Introduction

Bark beetles the size of a rice grain can have outbreaks with biome-scale impacts in boreal and temperate conifer forests (Raffa et al., 2008; Økland et al., 2011). For example, the Eurasian spruce bark beetle *Ips typographus* (L.) is considered the most destructive insect in Europe's conifer forests (Grégoire and Evans, 2004), and during 50 years (1950–2000) it has killed about 150 million m³ of Norway spruce in extensive outbreaks

(Schelhaas et al., 2003; Økland et al., 2012). Its main host tree is Norway spruce (*Picea abies* (L.) H Karsten), the most abundant conifer throughout northern Europe and in mountain ranges of central, southern and western Europe (Brus et al., 2012). At low population densities, the spruce bark beetle breeds in fresh windthrows or dying spruces, but cannot colonize healthy trees that are protected by effective constitutive and inducible defenses (Franceschi et al., 2005; Krokene, 2015). Extensive drought or windfall events, which occur sporadically in time and space, can trigger beetle outbreaks by lowering tree resistance or raising the population above the threshold density required to colonize and kill healthy trees (Netherer et al., 2015). Such outbreaks tend to last a few years,

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until the supply of suitable brood trees is exhausted or the drought ends and the trees recover their resistance (Økland and Bjørnstad, 2006; Kausrud et al., 2012). Management of outbreaks will benefit from a better basic understanding of bark beetle outbreak dynamics in windfall areas. To stop or slow down infestations we must for example know how to limit the progression of an outbreak once it has been initiated. Sometimes the volume of trees killed by the spruce bark beetle during an outbreak is many times higher than the volume of the windthrows that triggered the outbreak (Nikolov et al., 2014), while in other cases efficient management limits further progression of beetle-killing following windfall (Kärvemo et al., 2014a).

Outbreaks of the spruce bark beetle tend to form patches of killed trees across the forest landscape, as each beetle generation disperses to colonize new trees (Worrell, 1983; Kautz et al., 2011; Kärvemo et al., 2014b). Dispersal distances for the spruce bark beetle is often reported to follow strongly declining distance functions (Helland et al., 1989; Schlyter, 1992; Skarpaas and Økland, 2009). Similar declining functions, such as negative exponential and inverse power law functions, have also been reported for distances from old to new spruce bark beetle infestations in different parts of Europe, and most new spruce bark beetle infestations have been recorded within 500 m of the previous year's infestations (Wichmann and Ravn, 2001; Kautz et al., 2011; Stadelmann et al., 2014).

From a management perspective, however, the size of new infestation patches is also important, and although the number of new patches declines strongly with distance it is less clear how their size relates to the distance to previous years' patches. Intuitively, patch size could be expected to decrease with increasing distance, due to declining numbers of dispersing beetles with distance. However, a study of the spruce bark beetle in southern Germany reported no such effect on patch size (Kautz et al., 2011), and a recent Swedish study found only a weak influence of variables reflecting local beetle pressure (estimated by the size and proximity of last year's infestation patches) on the infestation risk in 100 × 100 m grid cells (Kärvemo et al., 2014b).

At the local level the risk of bark beetle infestations is generally considered to be a function of site/stand characteristics and local beetle pressure (Shore and Safranyik, 1992; Lausch et al., 2011; Stadelmann et al., 2013b; Withrow et al., 2013; Kärvemo et al., 2014b). The process by which new infestation patches are formed is not fully understood, even though a comprehensive literature including experiments and field studies indicate that the spatial pattern of infestation patches across the landscape is determined by beetle dispersal and colonization behavior, beetle host preferences, stand conditions and chemical interactions between trees and beetles (Netherer and Nopp-Mayr, 2005; Boone et al., 2011; Zhao et al., 2011; Schiebe et al., 2012; Hilszczanski et al., 2006). However, it is still a challenge to link our understanding of beetle–host tree interactions at small spatial and temporal scales with infestation patterns observed at greater scales (Lima and Zollner, 1996; Morales and Ellner, 2002). It is difficult to make exact predictions of the spatial distribution of new infestation patches during bark beetle outbreaks using pure statistical models based on site characteristics and local beetle pressure. An alternative approach may be to compare statistical models of empirical outbreak data with interactive simulation models incorporating the tree colonization behavior of individual beetles.

In the present study we explored the spatial patterns of new infestation patches formed during a severe spruce bark beetle outbreak in the Tatra National Park in Slovakia following an extensive windfall episode in 2004. We used empirical data of windthrows, patch sizes and inter-patch distances to analyze the progression of the outbreak and to identify the time of the transition from windfall-driven to patch-driven outbreak dynamics. The

patch-driven phase of the outbreak was analyzed in more detail using both empirical data and model simulations to explore two alternative hypotheses for how new infestation patches are formed: H0 – formation of new patches is determined by beetle densities following a pure dispersal process; H1 – formation of new patches is determined by beetle aggregation on individual trees during the dispersal process. To evaluate the model fit under hypotheses H0 and H1 we compared the results for both model-simulated infestations with empirical infestations.

2. Materials and methods

2.1. Study area

On the 19th of November in 2004 the heavy windstorm Alžbeta struck Slovakia and damaged roughly 5.3 million m³ of Norway spruce, which is almost the annual harvesting volume in Slovakia (reference period 1994–2003; cf. Kunca et al., 2012). In the following years, bark beetle populations increased rapidly in the impacted areas and during 2005–2010 more than 15 million m³ of spruce was killed or felled due to bark beetle attacks (Kunca et al., 2012). The Tatra National Park in northern Slovakia was most heavily affected by the storm, with >2.5 million m³ spruce damaged over 120 km² (Nikolov et al., 2014). Most of the windfelled volume was situated in the flatter areas at the foot of the High Tatra mountains and in valley floors. Due to the protection status of the park very little salvage logging of windfelled trees or sanitation felling of bark beetle infestations were carried out.

Our empirical data come from a 60 km² area with extensive bark beetle activity in the High Tatra mountains. The study area is spruce-dominated, with stands that mature and may become susceptible to bark beetle attacks from the age of 50 years (Nikolov et al., 2011). Our study area encompassed three closely connected valleys (Tichá, Kôprová and Važecká) in the central part of the Tatra National Park (Fig. 1), where approximately 51,000 m³ of windfelled trees that were left uncut triggered a bark beetle outbreak (Vakula et al., 2007). No major new windfall episodes occurred in the area during the study period and the spruce bark beetle was recorded to be univoltine.

2.2. Data collection and preparation

In 2005–2009, high-resolution aerial images in the visible and infrared spectra were taken of the study area at the end of each growing season in late September and early October. We used manual digitizing and comparison with aerial photographs in GIS to ensure a high accuracy of image classification, since the reliability of automated classification tends to be low in rugged terrains with varying light conditions (Heurich et al., 2010). Beetle-infested patches in the images were identified by the difference between red and green tree crowns, which became detectable 2–4 months after the beginning of infestations. The identified patches of beetle infestations and windfall were recorded using digitizing methods in ArcGIS 9.3 (ESRI Inc., California), see method descriptions in Nikolov et al. (2014) for details. The GIS data included more than 5000 polygon patches of beetle-killed forest from 2005 to 2009.

ArcGIS 9.3 was used to create polygon areas of the windfall area and the new infestation patches that developed each year, to determine patch sizes, and to measure distances from new infestation patches to the windfall area and to all infestation patches from the previous year (Nikolov et al., 2014). In addition, ground surveys were conducted in the years 2005–2007 to estimate the proportion of windfelled trees that were used or unused by bark beetles, or that were dry and unsuitable for bark beetle

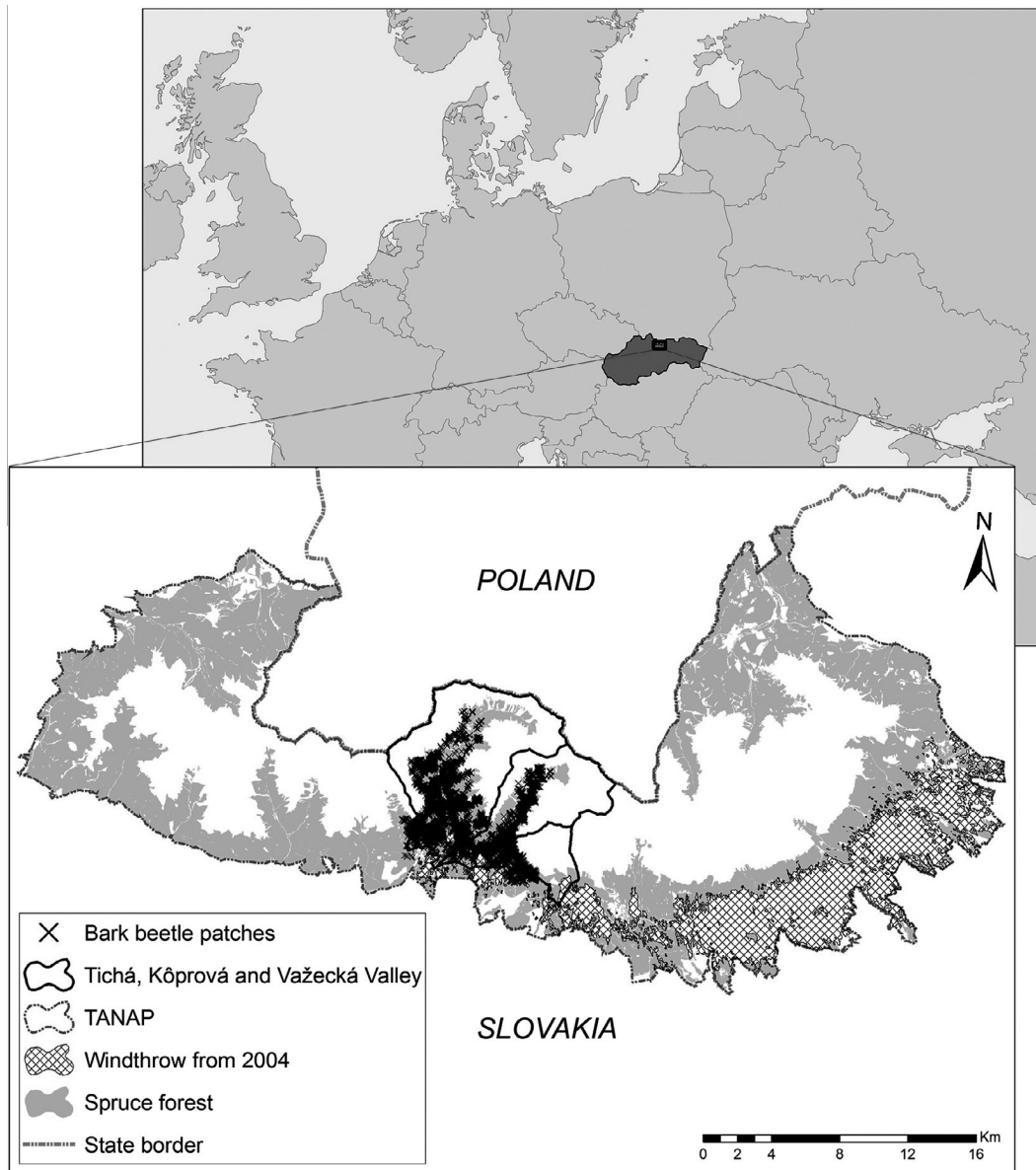


Fig. 1. The area of windfelled Norway spruce in the High Tatra mountains in 2004 and the study area in the valleys in the Tatra National Park (TANAP) that were most heavily affected by the ensuing bark beetle outbreak.

development. These estimates were based on transects through the windfall area, where trees in the transect were selected and debarked for counting the number of galleries (Vakula et al., 2007). Based on polygons recorded in ArcGIS 9.3, the distribution of distances from all infestation patches to the windfelled area and to the closest patch from the year before were plotted as histograms in the statistical software R (R Development Core Team, 2012). By comparing the shape of these histograms to the distance distribution found in a previous mark-recapture study of the spruce bark beetle (Botterweg, 1982), we got an indication whether new patches were formed by beetles from the windfall area or by beetles produced in infestation patches created the year before. We used two methods to estimate distances, because most distance methods have their disadvantages: (1) the shortest edge-to-edge distance between polygons and (2) centroid-based distances. Since the two methods gave a similar pattern, only edge-to-edge distances were used in the result presentation.

2.3. Beetle pressure function

We developed a 'beetle pressure function' (BPF) to study the functional relationship between patch size and beetle pressure (i.e. the number of beetles produced the year before within various distances from an infestation patch). Beetle pressure was estimated indirectly by using the area of beetle infestation patches. Since the study area consisted of a relatively homogenous spruce forest, we assumed as a simplification that the number of bark beetles produced in an infestation patch was proportional to patch area. Spatial variation in beetle production per area was assumed to be evened out since the BPF statistic was based on many infestation patches.

The 'beetle pressure function' (BPF) was calculated in the following way: for every new infestation patch in the dataset we recorded (1) its size and (2) the proportion of a surrounding circle area that was covered by beetle infestations in the previous year (Fig. 2). The infested circle area (2) was calculated for circles with

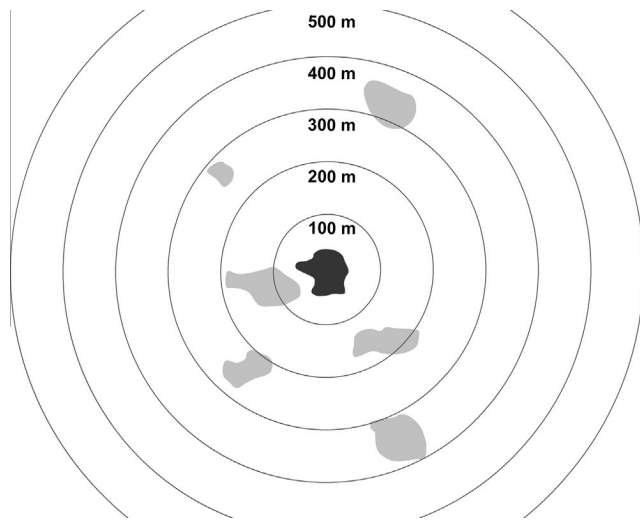


Fig. 2. For each new bark beetle infestation patch (black), local beetle pressure was estimated by calculating the proportion of a circle area surrounding the patch centroid that was covered by beetle infestations in the previous year (grey). Proportions were calculated for circle radii ranging from 0 to 2000 m.

increasing radius, using 100 m increments up to 2000 m. For all infestation patches each year, the BPF value was first calculated as the Spearman's rank correlation coefficient (Sokal and Rohlf, 1995) between (1) patch size and (2) the proportion of a 100 m radius circle being infested (BPF_{100}). BPF values were then calculated in a similar way for circles with increasing radius up to 2000 m (BPF_{200} , BPF_{300} , etc.) and plotted against the radius distance on the X-axis, giving a BPF curve for each year. BPF can attain values between 0 and 1, and for example a BPF value of 0.3 for $X = 300$ m (i.e. $BPF_{300} = 0.3$) in 2008 would correspond to the Spearman correlation between infestation patch sizes in 2008 and the proportion of surrounding circle areas of radius 300 m that were covered by beetle infestations in 2007.

Since beetle productivity is expected to differ between the windfall area and the infestation patches (Schroeder, 2010; Kärvelo et al., 2014a), we calculated BPF only for the years 2008 and 2009, when there were no longer any beetles reproducing in and spreading from the windfall of 2004. To test different models of patch development (see next section) the shape of the BPF curves for 2008–2009 was compared to BPF curves of simulation models based on alternative hypotheses for mechanisms of patch development.

2.4. Testing alternative models of patch development by simulation

To explore alternative hypotheses on possible mechanisms of patch development we developed two individual-based simulation models. Model variant H0 was based on a pure dispersal process, whereas model variant H1 also incorporated the beetles' aggregation behavior by including aggregation on individual trees. H1 also included a sensitivity analysis where we varied the number of aggregation trees in the landscape.

2.4.1. H0 – pure dispersal

In this model variant we let the patterns of beetle densities in the forest landscape after dispersal determine the position and size of new infestation patches. The extent of the simulation landscape was set to 5 km × 5 km. This size is somewhat smaller than the area of the empirical data (~7.7 km × 7.7 km), but this difference should not impact the comparison of beetle pressure operating at a smaller scale (within a radius of 2000 m). In the first model step,

100 simulated patches representing the previous year's beetle killing (i.e. source patches) were placed randomly in the landscape. The size of the source patches were drawn randomly from a distribution corresponding to the patch sizes in the empirical data. To find the distribution of patch sizes to be used in step 1, we fitted a gamma distribution to the empirical data of patch sizes with a density function

$$f(x) = 1/5421.473^{0.2121523} \Gamma(0.2121523) * x^{-0.787477} * e^{-(x/5421.473)} \quad (1)$$

where x is the patch sizes in m^2 and Γ is the Gamma function. In the simulation, the size of the source patches were drawn randomly from this function and the number of beetles dispersing from each source patch was set proportional to the patch size. Each individual beetle was assumed to spread with randomized direction θ from the center of the patch

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

The individual dispersal distances from the source patches were randomized from a dispersal kernel D based on mark-recapture data of the spruce bark beetle in a previous study by Botterweg (1982). The data from Botterweg's experiment 3 were fitted to an exponential distribution (Turchin and Thoeny, 1993). Thus, the density function D of dispersal distances x (in meter) and rate λ was

$$D(x) = \lambda e^{-\lambda(x)}, \quad (3)$$

where $\lambda = 0.006653853$

Based on the point patterns of beetles after dispersal, patches with high beetle densities were converted to polygons representing new infestation patches. To single out the patches with the highest beetle densities (and hence the highest likelihood of tree-killing) the density and quantile functions (package "stats" in R) were applied to the point pattern of beetle positions after dispersal. To determine the beetle density leading to tree-killing, we tested a range of values of "adjust" (sensitivity parameter of the density function) and quantile values. We found that setting "adjust" to 0.1 and the quantile level to 90% gave simulated patch sizes of killed trees within the ranges observed in the empirical data. Points falling within areas with a beetle density higher than the 90% quantile were kept and converted to polygons that were considered as the new patches of beetle-killed forest after dispersal and tree colonization (Fig. 3). The simulation script was formulated in R (R Development Core Team, 2012), and the R code for the conversion of point patterns to polygons is given in Appendix A.

The BPF curve for simulated data of H0, including quartiles, was calculated in the same way as described for the empirical data. The BPF curve for the simulated data was compared to the BPF curve for the empirical data for 2008 and 2009 using the Nash–Sutcliffe model efficiency coefficient E (Legates and McCabe Jr, 1999)

$$E = 1.0 - \frac{\sum_i^N (O_i - S_i)^2}{\sum_i^N (O_i - \bar{S})^2}, \quad (\text{exp1})$$

where O_i are the BPF values for the empirical data for 2008 or 2009, S_i are the BPF values for the simulated data of H0, and i is an index denoting the values of O_i and S_i from the shortest to the longest distance (N) along the x -axis of the BPF curve. E can take values in the range $(-\infty, 1]$, where positive values express the proportion of the empirical data that are explained by the model, and negative values indicate no correspondence at all between the compared data sets.

2.4.2. H1 – aggregation behavior

This model variant was similar to H0, but included attraction to individual aggregation trees in the forest landscape. When the first spruce bark beetles to land on a tree (the pioneer beetles) tunnel into the bark, they begin to produce aggregation pheromones that

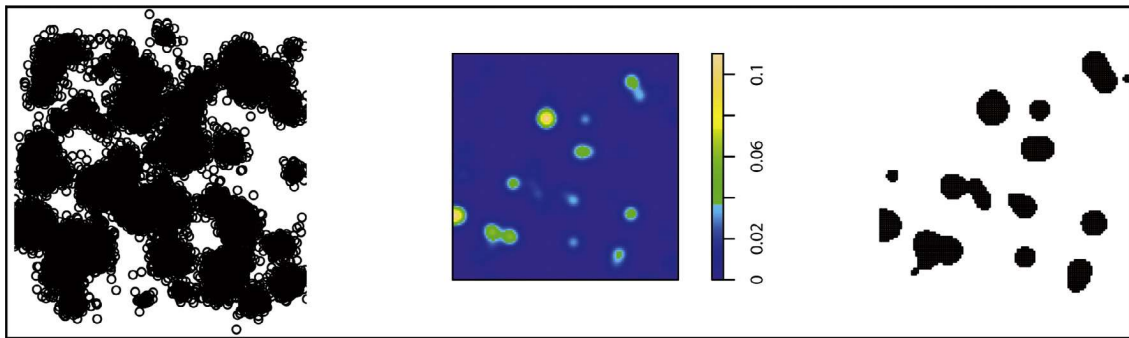


Fig. 3. Illustration of the spatial simulation procedure in R used to identify beetle-killed forest patches resulting from high beetle pressure. Left: distribution of beetle positions after dispersal. Middle: density function applied on beetle distribution after dispersal. Right: polygons converted from points falling within areas with beetle density higher than the 90% quantile.

may attract thousands of attacking beetles within a few days (Christiansen and Bakke, 1988). In our model, attraction of individual beetles to aggregation trees may include both primary attraction of pioneer beetles to host odors as well as secondary attraction of later attackers to the aggregation pheromones emitted by the pioneer beetles. Whether pioneer beetles are guided by host odors such as monoterpenes, or they select trees by random landing followed by post-landing choices (Saint-Germain et al., 2007; Schiebe et al., 2012), we assume that some trees in the forest landscape are more likely to be colonized than others, due to e.g. physiological stress that reduces their defense capacity. To simplify our model aggregation trees were placed randomly in the landscape and their density was scaled to the density of infestation patches observed in the empirical data.

Dispersing beetles were assumed to be attracted to an aggregation tree as soon as they entered its effective attraction radius (Schlyter, 1992). The effective attraction radius (R_{EA}) is much smaller than alternative measures of attraction to a pheromone source, such as the sampling range (R_S) or the attraction range (R_A) (Schlyter, 1992). R_S and R_A depend on how long the insect stays inside the range and are harder to measure, and therefore less useful in our individual-based simulation that requires a measure of attraction whenever an individual beetle gets close to an attraction source. R_{EA} was set to 0.5 m, which is close to the estimated R_{EA} for the spruce bark beetle when exposed to a medium pheromone dose at 1.9 m height ($R_{EA} = 0.57$ m), or the median value ($R_{EA} = 0.42$ m) of different canopy levels ranging from 0.7 m to 11.5 m (Byers et al., 1989).

When the breeding substrate of an aggregation tree is fully occupied, late-arriving beetles are known to switch their attack to neighboring trees (Schlyter and Anderbrant, 1989). Thus, in our model any extra beetles inside the attraction radius of a tree were redistributed to colonize the closest neighboring trees within the surrounding area. The distance to the farthest tree to be colonized was set proportional to the square root of the number of attracted beetles and scaled so that the surrounding area of colonized trees never exceeded the maximum patch size in the empirical data.

After this redistribution of beetles, patches with beetle densities above the 90% quantile were converted to polygons representing new patches of killed forest (Fig. 3 and Appendix A). In the same way as described for H0, the BPF curve including quartiles for simulated data of H1 was calculated and compared to BPF curves for the empirical data for 2008 and 2009 using the Nash–Sutcliffe model efficiency coefficient E .

Based on the patch distribution in the empirical data, we assumed that the density of randomly-placed aggregation trees in the simulations was about 3 trees per patch, corresponding to

an average of 97 m between neighboring aggregation trees. Since we did not have exact data for this variable, we varied the density of randomly-placed aggregation trees from 1 to 9 aggregation trees per patch to see how this influenced the values of correspondence (Nash–Sutcliffe model efficiency coefficient E) between model simulations and empirical data.

3. Results

3.1. Analyses of windfall area and infestation patches

The annual count of new infestation patches increased strongly over the observation period, while the annually infected area reached a maximum in 2008 and then declined in 2009 (Fig. 4A and B). The mean size of new infestation patches each year also varied over the course of the outbreak and peaked in 2007; however, the variation in patch size was very large in most years (Fig. 4C). According to the transect estimates, only a small proportion (11%) of the windfelled trees were infested in 2005, while most of them (72%) were colonized within 2006 (Fig. 4D). In the following year (2007), offspring from the large 2006 colonization of windthrows contributed to the biggest increase in area of new bark beetle infestations in the time series (Fig. 4B). In the spring 2007, almost none (<1%) of the windfelled trees were still suitable for bark beetle colonization, either because the bark had dried out or because the trees already had been utilized by the beetles (Fig. 4D). Thus, in 2008 and 2009 almost all new infestations originated from beetles produced in the previous years' infestation patches, with a negligible contribution from beetles developing in windfalls.

The distribution of distances from new infestation patches to the windfelled area or to the previous years' infestation patches indicated that a transition from windfall- to patch-driven outbreak dynamics took place between the third and fourth season after the windfall (Fig. 5). Most of the beetles that created new infestation patches in 2007 were probably produced in the windfall the year before (upper central bar plot). The distribution of distances from the windfall to new infestation patches in 2007 (upper left histogram) closely resembled the distribution of flight distances of individual beetles recorded in a previous mark-recapture experiment (Botterweg, 1982; dashed line in upper left histogram of Fig. 5). In contrast, the distribution of distances from the previous year's infestation patches to new infestation patches in 2007 (upper right histogram) included a large proportion of long distances (>500 m) and followed a more irregular distribution that clearly differed from the flight distances of individual beetles (dashed line). In the following two years (2008 and 2009), nearly all beetles infesting new patches must have originated from the

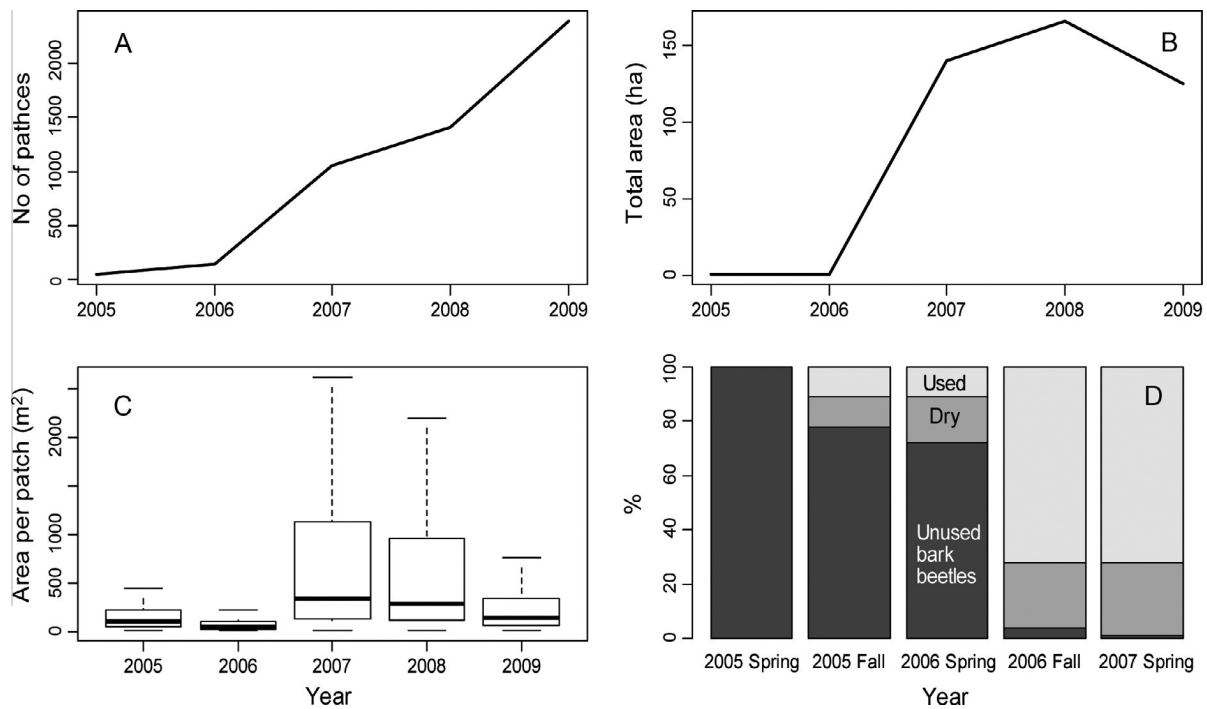


Fig. 4. Summary statistics of bark beetle infestations in the Tatra National Park from 2005 to 2009: total number of new infestation patches per year (A); total area of new infestation patches per year (B); boxplot of area of new infestation patches per year (C); proportion of wind-felled trees in the study area being used or unused by bark beetles, or being dry and unsuitable for bark beetle development in the period 2005–2007, based on transect estimations (Vakula et al., 2007) (D).

previous year's infestation patches, since less than 1% of the wind-falls were suitable for bark beetle colonization in 2007 and 2008 (middle and lower central bar plots in Fig. 5). Correspondingly, the distribution of distances from the windfall to new infestation patches in 2008 and 2009 (central left and lower left histogram, respectively) were irregular and differed clearly from the flight distances of individual beetles (dashed line). On the other hand, the distribution of distances to the previous years' infestation patches (central and lower right histograms) showed distinctly declining distributions that were closer to the flight distances of individual beetles (dashed lines).

3.2. Testing alternative models of patch development by simulation

We used the beetle pressure function (BPF) to study the functional relationship between patch size and the number of beetles produced within various distances from the patch in the previous year. It turned out that unlike the negative exponential distributions observed for distances from old to new infestation patches (Fig. 5), patch size was not a continuously declining function of beetle pressure in the surrounding area. The BPF values were highest within a 0–500 m radius, with a maximum at about 300 m (2008) or 400 m (2009) (Fig. 6A). This finding motivated the use of simulation models to explore possible mechanisms that could explain the observed patterns.

3.2.1. H0 – pure dispersal

If tree colonization is simulated as a process determined solely by the density of arriving beetles after dispersal, patch sizes of beetle-killed trees are expected to be strongly influenced by local beetle pressure. Accordingly, in our H0 simulation variant based on pure dispersal the influence of beetle pressure on patch size (BPF) showed a distinct decline by distance (Fig. 6B), corresponding to the negative exponential functions observed for the distances to new infestations (Fig. 5). This model variant did not show any

correspondence with the BPF curves observed for the empirical data (Fig. 6A), and the Nash–Sutcliffe model efficiency comparison between simulated and empirical BPF curves gave a maximum value $E = -4.97$, indicating no correspondence at all between the curves. Thus, our results do not support the hypothesis that patch development is a pure dispersal–diffusion process of the beetles.

3.2.2. H1 – aggregation behavior

A strong correspondence with empirical data was found when we implemented the beetles' aggregation behavior in the simulation model (Fig. 6C). Under this model dispersing beetles are attracted to aggregation trees when they enter the attraction range of such trees, and beetles that arrive at fully occupied trees switch their attack to neighboring trees. In the same way as for the empirical data, the BPF curve for the H1 simulation reached its highest values within a 0–500 m radius, with a maximum at about 300 m. The strongest correspondence between simulated and empirical data was found for data from 2008 with $E = 0.83$, which means that 83% of the variation in the empirical data was explained by the model. For 2009 data the correspondence was $E = 0.65$.

The BPF curve for simulation model H1 was sensitive to the density of aggregation trees in the landscape. The shape of the curve remained about the same under different aggregation tree densities, but the height of the curve and thereby the correspondence with the BPF curves of the empirical data varied (Fig. 6D). Comparing with the 2008 empirical data, model efficiency values were positive in the range 2450–2750 aggregation trees, while E values were negative outside this range. The maximum E value ($E = 0.83$) was found for 2650 aggregation trees in the study area, corresponding to an average of 97 m between aggregation trees or three aggregation trees per infestation patch. Comparing with the 2009 empirical data, model efficiency values were positive in the range 2100–2750 aggregation trees, with the maximum

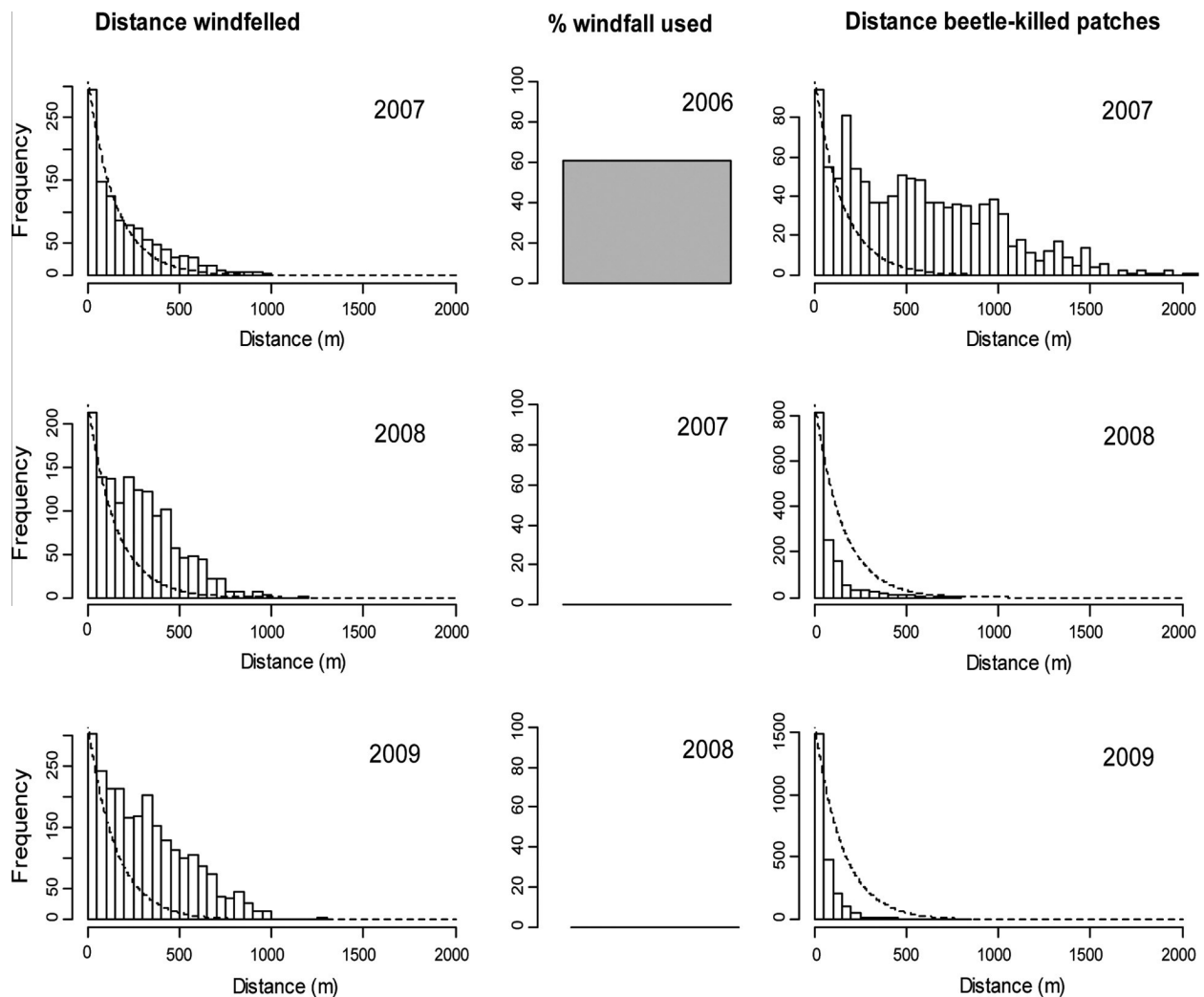


Fig. 5. Histograms of distances from each new bark beetle infestation patch in 2007, 2008, and 2009 to the border of the windfall area (left) and to the border of the closest infestation patch in the year before (right) in study area in the Tatra National Park. Dashed lines show the negative exponential density distribution of dispersal distances for individual bark beetles from a mark-recapture study by [Botterweg \(1982\)](#) (see Eq. (3)). For each year, the bar in the center shows the percentage of the windfelled spruce volume that was used for bark beetle development in the previous year (2006, 2007, and 2008, respectively).

E -value ($E = 0.65$) for the same density of aggregation trees as for the 2008 data (2650).

4. Discussion

Bark beetle infestations triggered by large windfall episodes may undergo a transition from windfall-driven to patch-driven outbreak dynamics. In our study area new infestation patches were predominantly initiated by beetles produced in windfelled substrates up until the third summer after the windfall (2007). During the two first seasons after the windfall (2005–2006), the beetles utilized an increasing proportion of the windfelled substrates ([Fig. 4D](#)), and during this phase the number of colonized windfelled trees appeared to be the key determinant for the distribution of new infestations the following year ([Fig. 5](#) upper histograms). Also [Kärvelo et al. \(2014a\)](#) found that the number of colonized windfelled trees was the most important variable influencing tree mortality in the years following a large windfall event. However, our results also indicated that when windfelled substrates became exhausted or unsuitable for beetle production, beetles produced in new infestation patches became the main driver of further infestations ([Fig. 5](#)). Efficient salvaging of windfelled trees the first

1–2 years after a storm may reduce or stop further infestations, because it helps keeping beetle numbers below the threshold density required to kill trees ([Berryman, 1982; Økland and Bjørnstad, 2006](#)). Apparently, the relative effect of salvage logging in each of the subsequent years depends on several factors, such as climate, voltinism and the degree of salvage logging in each of the years ([Stadelmann et al., 2013a; Kärvelo et al., 2014a](#)). In our study area with little salvage logging and univoltine beetle populations most of the beetle production in windfelled trees happened in the second summer after the windfall of November 2004 ([Fig. 4D](#)), which implies that efficient removal of windfelled trees before or during the summer 2006 probably would have reduced the risk of having a continued bark beetle outbreak ([Svensson, 2007; Kärvelo and Schroeder, 2010](#)). However, minimal salvaging of windfelled trees instead led to an outbreak sustained by beetles produced in new infestation patches, where total bark beetle damage during the first five years became approximately three times larger than the volume of uncleared windfelled trees ([Nikolov et al., 2014](#)).

Many factors influence the dynamics and spatial patterns of bark beetle infestations during the patch-driven outbreak phase, including bark beetle dispersal and colonization behavior ([Boone et al., 2011; Zhao et al., 2011; Schiebe et al., 2012](#)). Beetle dispersal

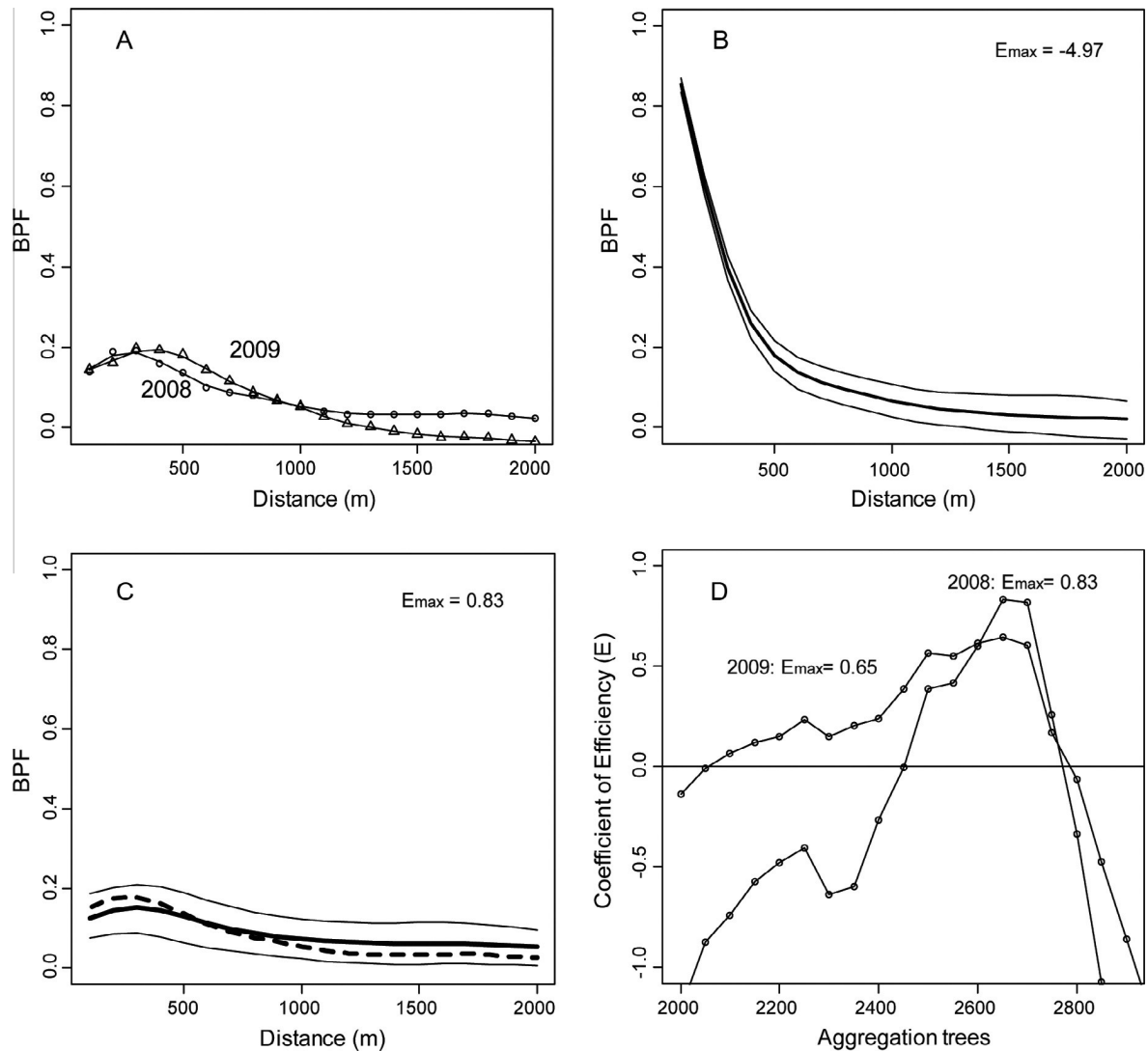


Fig. 6. Beetle pressure functions (BPF) for new bark beetle infestation patches observed in 2008 and 2009 (A), and for simulated infestation patches under hypothesis H0 based on a pure dispersal process (B), and hypothesis H1 incorporating the beetles' aggregation behavior (C). Enveloping curves in B and C denote upper and lower quartiles for BPF-values of repeated simulations, and dashed curve in C shows the BPF-curve for new bark beetle infestation patches observed in 2008. BPF was used to analyze the influence of estimated beetle pressure on patch sizes at various distances from new patches (see further explanations under 'methods') and (D) shows the correspondence (Nash-Sutcliffe model efficiency coefficient E) between the BPF-curves for the observed infestation patches in 2008 and 2009 and the BPF-curves for patches simulated under H1 when the number of aggregation trees in the study area (X -axis) was varied.

and tree colonization are in turn influenced by two main factors: characteristics of the bark beetle population itself, such as local beetle densities in the forest landscape, and interactions between local beetle densities and environmental variables related to topography and occurrence of susceptible host trees (Stadelmann et al., 2014). Both local beetle densities and beetle \times landscape interactions are strongly influenced by the beetles' ability to engage in pheromone-mediated mass-attacks on susceptible trees. This ensures concentration of local beetle populations on individual trees in synchronized attacks that rapidly may overwhelm the trees' total defense capacity (Franceschi et al., 2005; Økland and Bjørnstad, 2006; Raffa et al., 2008).

Local bark beetle densities clearly play some role in determining the spatial pattern of bark beetle infestations, as both beetle trap catches and the occurrence of new infestation patches usually are found to decrease with distance from source areas of beetle production (Botterweg, 1982; Helland et al., 1989; Schlyter, 1992; Turchin and Thoeny, 1993; Skarpaas and Økland, 2009; Stadelmann et al., 2014). Similarly, during the most intense

outbreak years (2008 and 2009) in our study area in Slovakia most new patches of beetle-killed trees occurred close to patches that had been killed by the beetles the year before (Fig. 5). This result also agrees with similar studies of spruce bark beetle infestations in e.g. Germany (Kautz et al., 2011) and Denmark (Wichmann and Ravn, 2001). Both our study and a study of inter-patch distances in Bavaria (Kautz et al., 2011) showed that more than 60% of new infestations occurred within 100 m of previous infestations.

Patch size, however, was not a monotonically declining function of beetle pressure in our study. The BPF curve of patch sizes in 2008 and 2009 increased to an optimum 300–400 m around new patches, after which it decreased (Fig. 6A). This result from our empirical data was not due to a high and spatially uniform background density of bark beetles across the landscape, as the frequency of infestation patches decreased rapidly with increasing distance from previously infested patches (Fig. 5). Similarly to our study, Swedish and German studies of spruce bark beetle infestations did not find patch size to be a negative exponential or other distinctly declining function of beetle pressure by distance

(Kautz et al., 2011; Kärvelo et al., 2014b). The shape of the BPF curves from 2008 and 2009 (Fig. 6A) was apparently not caused by the heterogeneous size and irregular shapes of the beetle infestation polygons. Our simulation experiment of patch development assuming a pure dispersal–diffusion process (H0) was based on irregularly shaped infestation polygons of heterogeneous size, and the BPF curves from that experiment had a negative exponential shape (Fig. 6B). The lack of fit between our model hypothesis H0, incorporating pure beetle dispersal, and our empirical data suggests that mechanisms other than pure beetle dispersal–diffusion are likely to be important for patch development.

The size distribution of beetle-killed patches may be influenced by the size distribution of forest stands available for attack. Both the volume and age of available host trees are important determinants for bark beetle infestations (Worrell, 1983; Klutsch et al., 2009; Jakuš et al., 2011; Kärvelo et al., 2014b). The spruce bark beetle does for example prefer mature spruce stands, and attack risk is positively correlated with the standing volume of spruce trees per hectare, up to a level corresponding to the standing volume in a mature forest (Kärvelo et al., 2014b). However, the distribution of mature spruce stands in our study area was very even and probably not important in shaping our BPF curves. Mature spruce (>50 years) covered 88.4% of the study area and the average age of the spruce forests in the area was 86 years (according to Slovakian forest inventory data from 2007).

Other factors that may influence the spatial distribution and sizes of bark beetle-killed forest patches are the coverage of deciduous trees, site topography, factors affecting trees water status, and various other factors that may stress the trees. Non-host volatiles from deciduous trees may affect the search and attack behavior of the spruce bark beetle (Zhang and Schlyter, 2004; Kärvelo et al., 2014b), but since the proportion of deciduous trees in our study area was very low this factor probably had negligible impact on the observed attack pattern. Similarly, steepness was probably not an important determinant of variation in patch size, since almost all the stands available for attack during the expansion phase of the outbreak (2007–2009) were in hillsides with similar steepness. More geographically fine-scaled predisposing factors for bark beetle attack include aspect (Worrell, 1983; Stadelmann et al., 2014), soil conditions (Worrell, 1983; Klutsch et al., 2009), stand vigor (Coops et al., 2009), and sudden stress (Führer et al., 1997) operating at the stand or tree-group level, and nutrient content, tree vigor, defense capacity, and drought stress (Reid and Robb, 1999; Hedgren and Schroeder, 2004; Wallin and Raffa, 2004; Coops et al., 2009; Jakuš et al., 2011; Schiebe et al., 2012; Netherer et al., 2015) operating at the individual tree level. Unfortunately, there are no data available to test the influence of such fine-scale factors on the extent of infestation patches in our study area.

As discussed above, the spruce bark beetles' aggregation behavior may be a key determinant for the distribution of beetle-killed forest patches. Pheromone-mediated aggregation is an essential component in the biology of the spruce bark beetle and is important for the initiation and expansion of infestation patches. Incorporating beetle aggregation to certain trees and switching of attack to neighboring trees into our simulation model (hypothesis H1) gave a similarly shaped BPF curve as for the empirical data from 2008 and 2009. A strong correspondence with empirical data was observed when using an average of three aggregation trees per infestation patch, which may be a biologically realistic density in our study area. Since our model simulations based on aggregation behavior gave a strong correspondence with the empirical data, it can be concluded that hypothesis 1 is a biologically plausible model for patch development. Although these similarities of patterns are only suggestive evidence for a role of beetle aggregation, our results indicate that the spruce bark beetle's aggregation

behavior may be one important explanation for the empirical observations of patch sizes. It is very difficult to obtain data for all the fine-scale environmental factors that may contribute to variation in patch sizes during region-wide bark beetle outbreaks, and further research is needed to integrate models of individual beetle behavior with spatial information about the forest environment into one comprehensive model system.

The model approach taken in this paper is proposed as an exploratory tool to assess whether important behavioral mechanisms of the spruce bark beetle may influence the patterns of killed forests in real landscapes. More mechanisms than those included in our models may of course be involved in the complex and interactive process of bark beetle host colonization and tree-killing, and it is possible that other factors than the beetles' aggregation behavior may produce a similar pattern. Additional factors that could be explored are for example laboratory results suggesting that very high beetle densities in some localities may yield offspring with lower weight and fat content (Anderbrant et al., 1985), which in turn may affect the beetles' flight performance (Botterweg, 1982) and their tolerance to tree defenses (Reid and Purcell, 2011). In addition, high densities of failed beetle attacks on individual trees during outbreaks might induce acquired resistance in these trees to new attacks the following summer (Erbilgin et al., 2006; Krokene et al., 2013).

5. Management implication

Our results demonstrate the advantages of removing storm-felled trees before a bark beetle outbreak makes the transition into the patch-driven outbreak phase, which is very difficult to control. The risk of 'igniting' patch-driven outbreak dynamics is reduced or eliminated if beetle production in windfelled trees is kept low enough to prevent the beetle population from increasing above the threshold required to kill trees (Kausrud et al., 2012; Kärvelo et al., 2014a). For univoltine beetle populations, it is particularly important that windfalls are removed no later than during the second summer after the windfall episode, since most of the beetle reproduction in windthrows in our study area took place that summer. By the third summer after the storm most of the windthrows were either already used or unsuitable for beetle production.

Our results also demonstrate how difficult it is to predict the size and spatial distribution of spruce bark beetle infestation patches when the outbreak has entered the patch-driven outbreak phase. The size of new infestation patches is not a simple function of beetle pressure from nearby infestation patches produced the previous year. This is partly because outbreak expansion is governed by the beetles' pheromone-coordinated mass-attack behavior. Initiation and expansion of infestation patches involves initial aggregation of beetles on susceptible trees followed by switching of attacks to neighboring trees. Although in principle it might be possible to identify all the aggregation trees in a forest landscape that can serve as starting points for patch development, it remains very difficult to predict how large individual infestation patches will become. Patch growth is influenced by complex interactions between bark beetle colonization behavior and site characteristics, including factors such as the size of the local beetle population, the density of aggregation trees, local weather conditions, topography, and soil conditions.

Acknowledgements

This work was supported by the Norwegian Institute of Bioeconomy Research (NIBIO), the Slovak Research and Development Agency based on the Agreement No. APVV-0707-12 for the Project

“Research of Disturbance Factors Affecting Long Lasting Development of Slovak Forest Health” and by the Operational Program of Research and Development, co-financed with the European Fund for Regional Development, Grant No. ITMS: 26220220109, “Forecasting-information systems for improving the effectiveness of forest management”. We thank Roger Bivand and Holger Lange for support with statistical methods, Matúš Kajba for assistance in processing GIS data, Andrej Gubka, Juraj Galko, Andrej Kunca, and Ján Ferenčík for valuable suggestions and discussions, and the reviewers for their helpful input that improved the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.12.007>.

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