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# Local colonization-extinction dynamics of a tree-killing bark beetle during a large-scale outbreak

S. Kärvemo,[1,2,]† V. Johansson,[1] M. Schroeder,[1] and T. Ranius[1]

[1]*Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 750 07, Uppsala, Sweden*

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**Abstract.** Forest pest insects may cause large-scale tree growth reductions and tree mortality during outbreaks. The large-scale development of outbreaks has frequently been studied, while the colonization-extinction dynamics during outbreaks is less known. We study the colonization-extinction dynamics of a severe tree-killing bark beetle, *Ips typographus*, during an outbreak across a 130 000 ha forest landscape in southern Sweden. We recorded annual colonization and extinction events in 1 ha pixels across the landscape by helicopter surveys during three consecutive years, and modeled colonization and extinction probabilities based on focal pixel quality, local population size, connectivity to surrounding beetle populations, and tree composition in the surrounding landscape. The local populations had a high turnover; 81–93% of all occupied pixels were the result of colonizations in the same year and the annual extinction rates were 84–90%. The colonization probability increased and the extinction probability decreased with increasing spruce (host-tree) volume in focal pixels and the connectivity. The fitted spatial scaling parameter of the connectivity measure suggested that the colonization probability was mainly affected by the number of surrounding occupied pixels within a few hundred meters. The colonization probability also decreased with increasing volume of birch (a nonhost) in the focal pixel, while the extinction probability decreased with increasing local population size. In conclusion, the local population size and quality of the focal pixel explained more of the colonization and extinction probability than the connectivity and composition of surrounding forest. The distribution of tree-killing bark beetles during outbreaks can be patchy and highly dynamic. Two reasons for this are the increased probability of successful attacks when exceeding a critical attack density and the fragmented distribution of large spruce volumes throughout the forest landscape.

**Key words:** connectivity; forest insect pest; *Ips typographus*; landscape; metapopulation; nonhost volatiles; Norway spruce; spatial dynamics.

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[2]Present address: Department of Wildlife, Fish and Environmental Studies, Swedish, University of Agricultural Sciences, 901 83, Umeå, Sweden.

† **E-mail:** simon.karvemo@slu.se

## Introduction

Forest pest insects may have outbreak periods during which they are so abundant that they cause large-scale tree growth reductions or mortality (Speight and Wainhouse 1989, Raffa et al. 2008) and consequently strongly impair timber production. Outbreaks often last several years and may cover millions of hectares. Most studies of the spatial dynamics of forest insect outbreaks have been conducted by determining where trees have been attacked each year at coarse grains (pixels ≥ 1 $\text{km}^2$; e.g., Peltonen et al. 2002, Gray 2004, Jepsen et al. 2009, Chapman et al. 2012). This may be the most relevant scale for species that attack most of their host trees over large contiguous areas. However, many insect outbreaks have patchy distributions even if their host trees are rather evenly distributed over large areas (Maron and Harrison 1997, Kautz et al. 2011). Especially for them, colonization-extinction studies at a finer grain are needed for the understanding of outbreak dynamics.

For outbreaking forest insects, little is known about the fine-grain colonization-extinction dynamics. Instead, many studies have considered the spatial pattern of occurrences (e.g., Radeloff et al. 2000, Robertson et al. 2007, Kautz et al. 2011, Kärvemo et al. 2014). Other studies have indeed observed colonizations and extinctions, but they have not investigated how these are related with environmental factors (Hedden and Billings 1979, Ayres et al. 2011, Colombari et al. 2013). Colonization-extinction dynamics have been studied more frequently in metapopulations of species confined to highly fragmented habitats. For these species, it has been found that the colonization probability increases with increasing quality and quantity of the local habitat (Eber and Brandl 1996, Franzén and Nilsson 2010) and that the extinction probability decreases with increasing local population size and habitat quality (Hanski 1998, Roland et al. 2000, Franzén and Nilsson 2010). Colonization and extinction probabilities may also be affected by connectivity to the surrounding occupied patches (Hanski 1998). Less is known about how the surrounding landscape composition influence colonizations, although it has been found to influence the dispersal (e.g., Roland et al. 2000, Ricketts 2001, Powell and Bentz 2014), and thus the probability of colonization (Gustafson and Gardner 1996) and extinction (Sjögren-Gulve and Ray 1996) of species.

In conifer forests, tree-killing bark beetles are usually the most economically important outbreaking species (Schelhaas et al. 2003, Raffa et al. 2008, Seidl et al. 2011). Their ecology makes them suitable for large-scale studies of fine-grain colonization-extinction dynamics during outbreaks because: (1) they mainly kill standing trees; (2) killed trees generally occur in well-defined groups (Ayres et al. 2011, Colombari et al. 2013, Kärvemo et al. 2014) which are easy to record over large landscapes by aerial surveys; and (3) each colonized tree is generally used by only one generation and colonization and extinction events can therefore be directly observed by comparing the spatial distributions of recently killed trees in consecutive years.

The aim of this study was to analyze the colonization-extinction dynamics of the spruce bark beetle (*Ips typographus* L.), which is the most serious forest insect pest in Europe (Grégoire and Evans 2004, Seidl et al. 2011). The study was conducted at 1-ha pixel resolution in a large managed forest landscape in southern Sweden during 3 yr of an extensive outbreak. Specifically, we assessed colonization and extinction rates, and analyzed effects of focal pixel quality, connectivity to local beetle populations, and surrounding forest composition on colonization and extinction probabilities. To our knowledge, this is the first study to evaluate factors influencing the colonization-extinction dynamics of an outbreaking forest insect over the full extent of a large-scale landscape.

## METHODS

### *Study species*

In Europe, the host tree of the spruce bark beetle is Norway spruce (*Picea abies* Karst). At nonoutbreak population levels, the spruce bark beetle reproduce in newly dead or weakened trees, while during outbreaks most individuals reproduce in living trees, resulting in tree mortality. In Fennoscandia, the spruce bark beetle is generally univoltine, i.e., it has one generation per year (Annila 1969), but each summer they usually have two broods in different trees. The new generation of beetles hibernates as adults under the bark of their brood trees or in the forest litter nearby. Thus, trees killed in the previous year represent dispersal sources when the flight period starts. Males initiate attacks by boring into the bark and releasing aggregation pheromones that strongly attract both males and females (Birgersson et al. 1984). The aggregation increases the probability of exceeding the critical threshold of attack density required for overcoming defenses of living trees (Mulock and Christiansen 1986, Nelson and Lewis 2008). Attracted beetles may switch their attack to neighboring trees and consequently trees are usually killed in aggregated groups (Schlyter and Anderbrant 1989).

### *Study area*

The study was conducted from 2007 to 2009 in a 130 000 ha area in southern Sweden (Fig. 1), during a large spruce bark beetle outbreak triggered by a storm, which felled 70 million $m^3$ of timber in January 2005 (Svensson 2007). This breeding material initiated spruce bark beetle outbreak, resulting in a total volume of 4 million $m^3$ of killed standing spruce trees between 2006 and 2011 (Kärvemo and Schroeder 2010, Lennart Svensson, *personal communication*). The tree mortality started at 1.6 million $m^3$ in the second summer after the storm (2006) and thereafter decreased to 0.8, 0.7, and 0.2–0.3 million $m^3$ in 2007, 2008, and 2009–2011, respectively. The forests are dominated by even-aged stands of Norway spruce (*Picea abies* L.) and Scots pine (*Pinus sylvestris* L.), which are thinned two or three times before final harvest by clear-cutting at an age of 60–80 yr. Birches (*Betula pendula* Roth. and *B. pubescens* Ehrh.) are the most common deciduous tree species. More than 99% of the productive forest land within the study area is managed. We divided the study area into 1-ha pixels. Pixels with spruces and with a stand age of >30 yr were regarded as possible habitats for spruce bark beetle, while younger trees have too thin bark (Grünwald 1986). About 68% (~88 000) of the pixels met these criteria, with slight variations among years because stands in some pixels were clear-felled. The mean spruce volume in the pixels was 115 $m^3 \cdot ha^{-1}$ (Table 1). The soil in 70% of the area consists of fluvio-glacial till and the area is rather flat with a mean elevation above sea level of 165.5 m (SD = 19.5).

### *Colonizations and extinctions*

We assessed local colonizations and extinctions of spruce bark beetles in 2008 and 2009, as manifested by the appearance of trees killed in the current year in a pixel where no trees were killed in the previous year (colonization), and the absence of current-year-killed trees in a pixel that was occupied the previous year (extinction). Thus, local extinction does not necessarily mean that the beetles produced in the killed trees have died; they could as well have dispersed

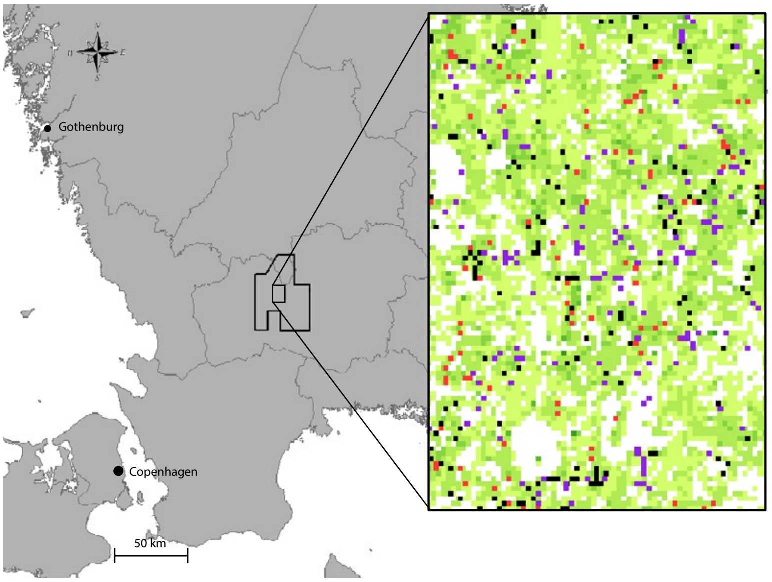

Fig. 1. The study area in southern Sweden and a more detailed view of part of it, where each pixel represents 1 ha. For the online version: green represent nonoccupied pixels with suitable forest (i.e., >30 yr) habitat (darker green = higher spruce volumes), red, black, and violet represent pixels occupied by the spruce bark beetle *Ips typographus* in 2007, 2008, and 2009, respectively. White represents nonhabitat, not included in the analyzes.

Table 1. The mean, median, and range values of the focal pixel variables.

| | 2008 | | | 2009 | | |
|---|---|---|---|---|---|---|
| Pixel variables | Mean | Median | Range | Mean | Median | Range |
| Volume of spruce ($m^3 \cdot ha^{-1}$) | 114.8 | 108.7 | 1–594 | 114.6 | 108.3 | 1–594 |
| Volume of birch ($m^3 \cdot ha^{-1}$) | 22.2 | 20.6 | 0–187 | 22.2 | 20.6 | 0–187 |
| Forest edge (presence/absence)† | 0.39 | – | – | 0.39 | – | – |
| Local population size (no. of killed trees)‡ | 13.8 | 7.1 | 7.1–160.2 | 10.4 | 7.1 | 7.1–71.4 |

† Presence and absence data was set to 1 and 0 in the analyses, respectively. Median and range are not given.
‡ The number of killed trees in the previous year, i.e., 2007 in model 2008 and 2008 in model 2009.

and contributed to tree killing in other pixels. Trees that had been killed in the current year by spruce bark beetles were surveyed by helicopter by the Swedish Forest Agency in September 2007, 2008, and 2009. Current-year attacks were identified by the color of the tree crowns and classified into one of four group size classes: 5–10, 11–25, 26–50, and 51–100 killed trees. The entire study area was surveyed by south–north facing transects and detours were conducted to visit the groups included in the study. The distance between each transect was approximately 800 m and the mean flight height of the helicopter was 214 m (SD = 22 m). To validate the survey's accuracy, 163 of the groups of killed trees recorded by the helicopter survey in 2007 were randomly chosen and inspected from the ground. On the killed trees, bark up to 2.5 m height was checked for spruce bark beetle galleries and living adults. If higher parts of the stems had been debarked by woodpeckers they were checked for galleries, and the ground around them was checked for pieces of bark. Of 1620 inspected trees, 1347 (83%) were confirmed to have been attacked by the spruce bark beetle in the current year, but this probably underestimates the beetle's presence since some attacks higher up in killed trees with all bark remaining could not be confirmed. This shows that the potential problem of false positives is small in our data. The potential problem of false negatives should also be small because groups of killed trees are very apparent from helicopter at the low flying altitude and high density of transects used in the survey. Moreover, we did not find any undetected groups during the ground survey for false positives. The difference between the helicopter and ground GPS readings was 22.2 m (SD = 15.2 m, $n$ = 163). It was not possible to record colonized wind-felled trees in the helicopter survey. However, this should not markedly have influenced the results, because there was only one storm-felling episode during the study period (in January 2007) and this storm event was much smaller than the one triggering the outbreak and mainly resulted in downed trees at stand edges of which most were removed during the winter. The survey data were converted to raster layers with 1-ha pixel resolution. As a proxy of population size, we converted tree group sizes to geometric means (7.1, 16.6, 36.1, and 71.4 for the four size classes, respectively) and summed them for each pixel. We used the geometric mean as the distribution within each class was skewed toward small numbers.

### Explanatory variables

The colonization and extinction probabilities were analyzed separately in relation to four focal pixel variables, two connectivity variables, and two variables reflecting the forest composition in the surrounding landscape. The focal pixel variables were: (1) volume of spruce and its squared term; (2) volume of birch (a nonhost tree species); (3) presence of recently created spruce forest edges; and (4) local population size in the previous year (Table 1). The last variable was only tested in the extinction models. The connectivity variables were: (1) connectivity to surrounding occupied pixels in the previous year; and (2) in the current year. The surrounding forest composition variables were: (1) spruce volume in the surrounding pixels; and (2) birch volume in the surrounding pixels.

The reasons why we tested these variables were as follows: Habitat quality has often been found to be the most important factor explaining colonization and local extinction probabilities (e.g., Franzén and Nilsson 2010, Fedrowitz et al. 2012), and studies of occurrence patterns suggest that pixel quality is important also for the spruce bark beetle (Netherer and Nopp-Mayr 2005, Overbeck and Schmidt 2012, Kärvemo et al. 2014). The squared term of spruce volume in the focal pixel was included in the colonization models to capture a possible nonlinear relationship that has been indicated in previous studies (Overbeck and Schmidt 2012, Kärvemo et al. 2014). The volume of birch was included because attraction and colonization of the spruce bark beetle have experimentally been shown to be affected by olfactory compounds from birch (Byers et al. 1998, Zhang and Schlyter 2004, Schiebe et al. 2011). The presence of newly created edges was included because the risk of attacks by spruce bark beetles are higher for trees in forest edges, possibly because they are more stressed, than for trees in the interior of stands (Peltonen 1999, Schroeder and Lindelöw 2002). The previous year's local population size (as estimated by the number of killed trees) was included in the extinction models because for tree-killing bark beetles, a larger beetle population size increases the probability of exceeding the threshold of beetle numbers required to overcome tree defenses (Raffa and Berryman 1983). Connectivity often increases the colonization probability in highly fragmented populations (Hanski 1998) and previous studies of the spruce bark beetle have demonstrated that infestation risks are highest close to sites of major infestations in the previous year (Wichmann and Ravn 2001, Kautz et al. 2011). Connectivity to current year's local populations may influence immigration to the focal pixel. The habitat is believed to influence the bark beetles' dispersal efficiency, and the composition of the surrounding landscape may thus also affect colonization probability (Shore et al. 2010, Simard et al. 2012), but this has rarely been tested (see however Powell and Bentz 2014). Accordingly, we tested the effect of both the host tree species (spruce) and a nonhost (birch), because bark beetles may be attracted to host-specific kairomones (Byers 1995) and repelled by nonhost volatiles (Borden et al. 1998, Jactel et al. 2001, Zhang and Schlyter 2004).

Data on spruce and birch volumes were accessed from the 2005 kNN maps of forest land in Sweden, which were derived from interpretations of satellite images, evaluated using data recorded on the ground, packaged as raster layers with 25 × 25 m resolution (Reese et al. 2003) and then aggregated to 100 × 100 m by averaging. Clear-cut edges up to 5 yr old were identified from annual interpretations of satellite images conducted by the Swedish Forest Agency (Thorell 2006) and quantified by presence or absence within each pixel.

Connectivity to surrounding occupied pixels ($S_i$) was calculated as follows:

$$S_i = \sum_{j=1}^{n} e^{-\alpha d_{ij}} A_j \tag{1}$$

where $\alpha$ is a model parameter regulating the spatial scaling, $d_{ij}$ is the distance in meters between the center of the focal pixel $i$ and the center of pixel $j$, $A_j$ is the number of killed trees in pixel $j$, and $n$ is the number of pixels within 1000 m. We calculated connectivity to the number of killed trees in the previous year and the current year separately. When calculating surrounding forest composition (spruce and birch volumes, separately), we used the same equation, but with $A_j$ representing the spruce or birch volume in pixel $j$. Hence, in total, we tested four different spatial variables based on Eq. (1): two measures reflecting connectivity to spruce bark beetle populations, and two measures reflecting the surrounding forest composition.

The connectivity measures were weighed by distance and population size of the surrounding occupied pixels (Eq. [1]), because these two factors are likely to influence the probability of local beetle populations reaching threshold sizes required to successfully colonize host trees (Kausrud et al. 2012). When fitting each model, we optimized the parameter $\alpha$ (as described in Statistical analyzes) for both connectivity variables simultaneously, to ensure the spatial weighing was the same for both measures. We then used this optimized $\alpha$ when testing the two variables reflecting surrounding forest composition. In the 2008 extinction model, neither of the connectivity variables improved the Akaike Information Criterion (AIC). We concluded that immigration

Table 2. Distribution (percentages) of occupied pixels, colonizations and extinctions into five population size (number of killed trees per pixel) classes. Colonizations and extinctions for 2008 and 2009 are based from occupations in 2007 and 2008, respectively. "All" is the percentage of the pixels that are occupied, colonized and extinct, "Sum" is the number of occupied, colonized, and extinct pixels, while "Total" is the number of pixels with Norway spruce and a stand age >30 yr in the study area.

|  | Occupied (%) |  |  | Colonizations (%) |  | Extinctions (%) |  |
|---|---|---|---|---|---|---|---|
| Population size | 2007 | 2008 | 2009 | 2008 | 2009 | 2008 | 2009 |
| 5–10 | 66.4 | 79.1 | 82.0 | 79.5 | 84.1 | 68.3 | 80.5 |
| 11–25 | 23.4 | 17.0 | 15.9 | 16.6 | 14.0 | 22.5 | 16.1 |
| 26–50 | 6.7 | 2.3 | 1.6 | 2.3 | 1.4 | 6.6 | 1.8 |
| 51–100 | 3.0 | 1.6 | 0.5 | 1.6 | 0.4 | 2.4 | 1.5 |
| 101–200 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 |
| All (5–200) | 1.3 | 2.1 | 1.9 | 2.0 | 1.5 | 89.6 | 83.5 |
| Sum (no. pixels) | 1030 | 1639 | 1411 | 1532 | 1141 | 923 | 1369 |
| Total (no. pixels) | 76 851 | 76 346 | 75 602 | 75 316 | 74 196 | 1030 | 1639 |

from other pixels was not important in this model, so we also excluded surrounding forest variables from the final model. In the 2009 extinction model, previous-year connectivity was excluded from the model due to a strong collinearity with current-year connectivity, and because the current-year connectivity had a stronger relationship with the extinction risk. When calculating the connectivity and surrounding forest variables, we included pixels within 1000 m of the focal pixel, covering previously reported zones of increased infestation risk around bark beetle populations by a wide margin (Wichmann and Ravn 2001, Kautz et al. 2011). To not underestimate the connectivity of pixels close to the border of the landscape, we established a 1000 m wide buffer zone inside the outer boundary of the study area. This left a mean number of 76 266 spruce pixels (defined as described above) over the 3 yr, for which colonization and extinction probabilities were analyzed (Table 2).

### *Statistical analyzes*

We modeled colonization and extinction probabilities using generalized linear models with logit link functions. We fitted four models: one colonization and one extinction model for each year (i.e., from 2007 to 2008 and from 2008 to 2009). For each model, we first included the characteristics of each pixel and the connectivity measures. In this step, we estimated the spatial scaling parameter $\alpha$ between 0 and 0.1, using an optimization function, where $\alpha = 0$ means giving the same weight to all surrounding pixels within 1000 m and $\alpha = 0.1$ means giving occupied pixels further away than the closest ones a very low weight (Johansson et al. 2013). We then extended the model with the two variables reflecting surrounding forest composition. These full models were then reduced (based on AIC) using the R function step (R Development Core Team 2012); the final models were the ones with the lowest AIC values. All continuous variables were standardized. The local population size was log-transformed to improve normality. Collinearity among explanatory variables was assessed by pairwise Pearson correlation tests, and for all correlations $r < 0.6$. It has been suggested that if $r < 0.7$, the correlations should not severely distort model estimations (Dormann et al. 2013). We approximated the importance of each of the variables from the increases in AIC when they were removed one at a time from the final model (i.e., we compared the AIC of the best model with the AIC of a model where the variable of interest had been removed). All data were processed in Arcmap (ArcGIS 10; ESRI, Redland, California, USA) and R version 3.0.1 (R Development Core Team 2012).

## RESULTS

The percentage of pixels occupied by spruce bark beetles varied between 1.3% and 2.1% during the three study years (Table 2). The occupied pixels were rather homogenously scattered across the landscape (Fig. 1). Most of them (66–82%) were small (≤10 killed trees; Table 2). The colonization rate was 1.5–2.0% and the extinction rate was 83.5–89.6% (Table 2). Most of the occupied pixels were colonized in the current year: 93.5% in 2008 and 80.9% in 2009.

### *Colonizations*

Characteristics of the focal pixel were the most important factors explaining colonizations, based on the increase in AIC when removing them from the best model (Fig. 2). The most important pixel characteristic explaining colonization probability was spruce volume, and the probability was several times higher in pixels with high spruce volumes compared to those with lower volumes (Fig. 3). However, the colonization probability leveled off at about 200 $m^3 \cdot ha^{-1}$ (Fig. 3), which is captured by the negative relationship with the squared term (Fig. 2). The colonization probability decreased with increasing volume of birch, and increased if the pixel included newly created forest edges (Figs. 2 and 3). The colonization probability also increased with increasing connectivity, both to current-year and previous-year occupied pixels (Figs. 2 and 3), while the surrounding forest composition had a weak and non-consistent effect. Estimates of the spatial scaling parameter $\alpha$ of the connectivity measures, corresponded to distribution kernels with mean distances of 278 m (95% CI: 222–333 m) for 2008 and 111 m (95% CI: 91–143 m) for 2009. The colonization models explained 9.2% and 7.6% of the deviance for 2008 and 2009, respectively.

### *Extinctions*

In both years, the extinction probability decreased with increasing local population size and volume of spruce (Fig. 2 and 4). In the 2009 model, extinction probability was negatively related to current-year connectivity (Fig. 2). Extinction probability increased with increasing surrounding spruce volumes while surrounding birch had a negative effect (Fig. 2). For the spatial scaling parameter ($\alpha$) of the connectivity measures, the best fitted value was zero, which means that all pixels within 1000 m are given the same weight. The extinction models had generally low explanatory power; they only explained 5.6% and 2.2% of the deviance for 2008 and 2009, respectively.

## DISCUSSION

We show that during outbreaks, tree-killing bark beetles can occur scattered across the landscape in relatively small local populations with a high turnover. The effect of the variables in the two study years showed convincingly similar patterns. The local colonization-extinction dynamics are mainly explained by the habitat quality and the local population size the year before and connectivity to surrounding occupied pixels, but to some extent also by the composition of the surrounding forest.

The models were relatively poor in explaining local colonizations and extinctions. This may be because the spatial dynamics of the spruce bark beetles also are influenced by stochastic processes such as random events affecting migrating beetles or interactions between weather and forest conditions. Moreover, we only included patches which had suitable habitat (i.e., mature stands of >30 yr), which together with the fact that we studied a region that is topographically and climatically homogenous, decrease the variation in data. It may also be that the bark beetle–host interactions are affected by other factors from which we lack data. For instance, the attack of trees are affected by the insect physiological state, population density, and the physiological state of the trees (Raffa et al. 2008, Raffa 2014, Netherer et al. 2015). In addition, the importance of variables may change during outbreaks and previous spatio-temporal models of bark beetle outbreaks have shown higher explanatory power at the earliest outbreak phase (DeRose and Long 2012, Bone et al. 2013, Walter and Platt 2013). This study lacks data from the early and late outbreak years. Nevertheless, this study has increased the understanding of the fine grain colonization-extinction dynamics of outbreaking insects.

### *Colonizations*

The habitat quality of the focal pixel had a stronger effect on colonization probability than the connectivity and the surrounding forest

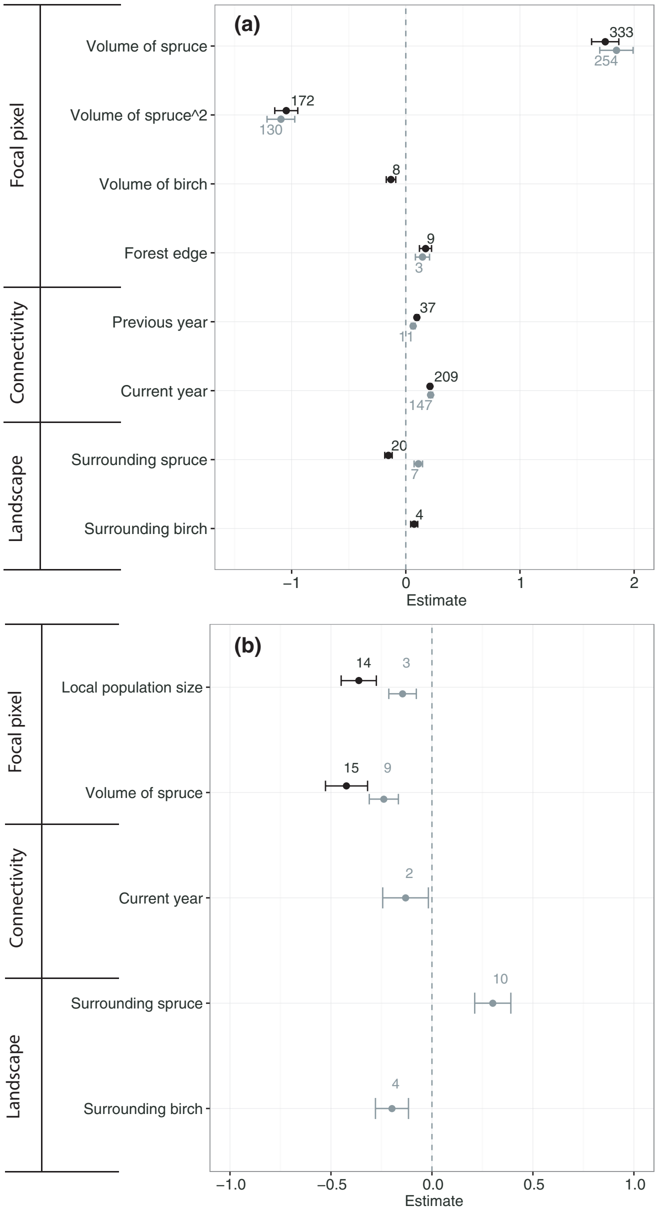

Fig. 2. Parameter estimates (±SE) of the explanatory variables and the reduction in AIC when removing the variables (one by one) from the best model (ΔAIC; numbers above the points) in the (a) colonization models and (b) extinction models of the spruce bark beetle *Ips typographus*. Black and gray bars represent estimates for 2008 models and 2009 models, respectively.

composition (Fig. 2.). The most important pixel characteristic was spruce volume, and there may be at least three reasons why it affects the colonization probability. First, the probability of beetles finding a susceptible host tree within a pixel increases with spruce density. Susceptible trees may be trees with reduced defenses or other characteristics, which increase the probability of a successful initiation of colonization (Raffa et al. 2008, Raffa 2014, Netherer et al. 2015). Second, the spruce bark beetle prefers large trees with thick bark (Grünwald 1986), and such trees are more frequent in older forest with a higher total spruce volume. Third, high

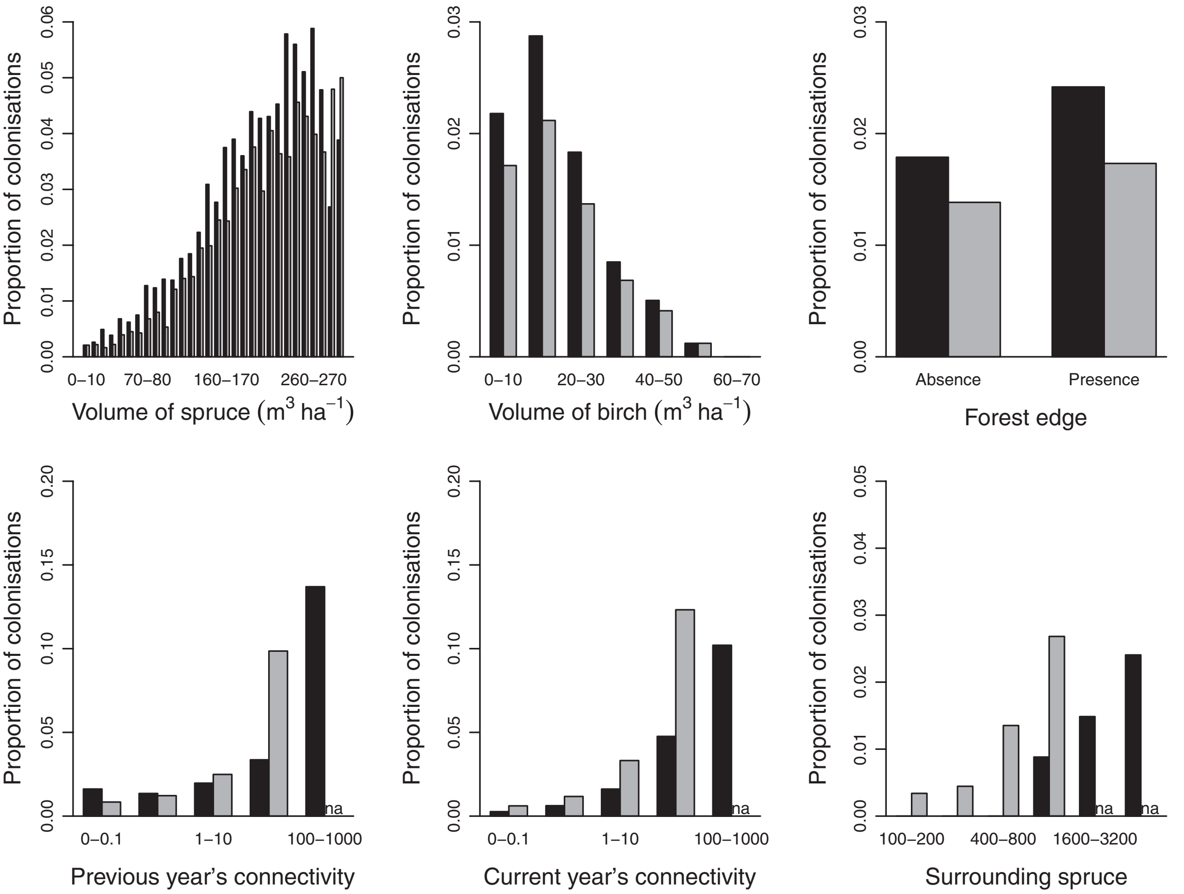

Fig. 3. The proportions of pixels colonized by the spruce bark beetle *Ips typogaphus* in relation with explanatory variables. Data are presented for explanatory variables with a ΔAIC > 5. Black and gray bars represent estimates from 2008 and 2009 data, respectively. na = no data.

densities of spruce trees increase the probability of beetles switching attacks to neighboring trees, resulting in groups of killed trees (in our surveys only groups with at least five killed trees were registered as occurrences). Also in other insect species, abundance of host plants are positively associated with colonization probabilities, as shown in examples of butterflies (Fleishman et al. 2002), bees (Franzén and Nilsson 2010) and parasitoid wasps (Andersson et al. 2013). We have found that the positive relationship between host volumes and the probability of colonization levels off at high densities, which is consistent with previous observations of a declining positive effect of tree ages and tree volume (which is strongly correlated) on spruce bark beetle-mediated tree mortality (Netherer and Nopp-Mayr 2005, Overbeck and Schmidt 2012, Kärvemo et al. 2014). Such patterns probably arise because where spruce volumes have exceeded a certain threshold density, suitable large-diameter spruces are so abundant that they do not limit the bark beetle colonization probability.

The presence of forest edges and birch volume were two other focal pixel characteristics also affecting the colonization probability. The presence of edge had a positive effect; edge trees may be more stressed than trees in the interior of stands (Peltonen 1999), which make them more susceptible for bark beetle colonization. High birch volumes in the focal pixels instead decreased the colonization probability, and the reason for this was probably not a negative correlation between birch and spruce volume, since it was weak ($r^2 = -0.22$ [2008] and −0.21 [2009]). Instead,

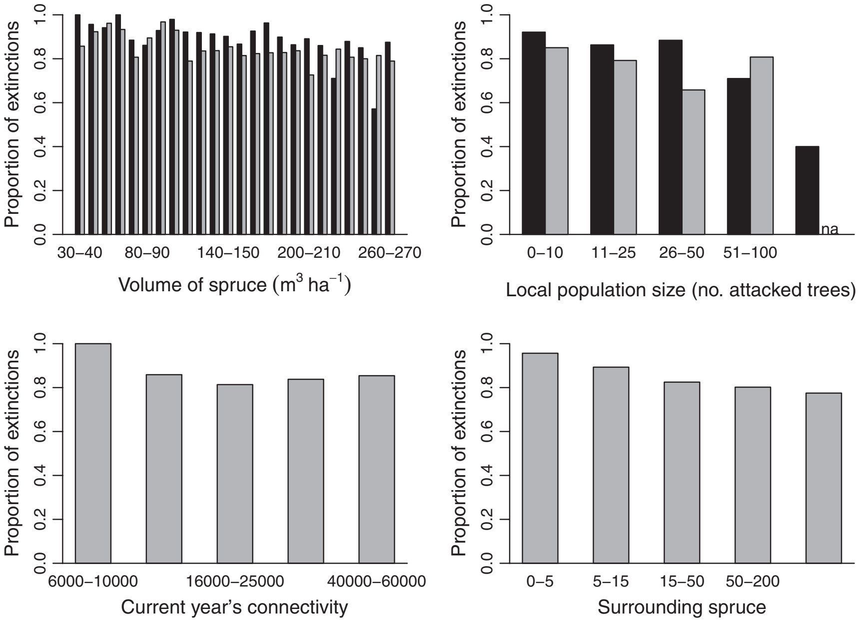

Fig. 4. The proportions of extinctions by the spruce bark beetle *Ips typogaphus* in relation with explanatory variables. Limits of ΔAIC, bar colors, and na represents the same as in Fig. 3.

it may be because nonhost volatiles from deciduous trees inhibit pheromone responses of bark beetles (e.g., Borden et al. 1998, Jactel et al. 2001), including the spruce bark beetle (e.g., Zhang and Schlyter 2004, Schiebe et al. 2012). To our knowledge, this is the first field study that finds a negative relationship between nonhost trees and colonization probability for tree-killing bark beetles. The result agrees with studies showing lower herbivory in host-trees located in mixed forests (Jactel and Brockerhoff 2007), and constitutes an argument for mixing tree species instead of creating monocultures (Jactel et al. 2001).

The colonization probability was explained by both the current-year and the previous-year connectivity. The fitted spatial scaling parameter of the connectivity measure ($\alpha$) suggested that the colonization probability was mainly affected by the number of surrounding occupied pixels within a few hundred meters. The effect of previous-year connectivity was expected, since it clearly reflects the number and size of local populations that may act as dispersal sources when the flight period starts in the spring. Current-year connectivity may also reflect the presence of dispersal sources, because most beetles will leave the tree in which they established their first brood to establish a second brood somewhere else later in the summer (Öhrn et al. 2014). A positive relationship between connectivity and colonization probability has been observed in many systems, especially for rare species in highly fragmented habitats, due to dispersal limitation (Hanski 1998). However, the spruce bark beetles have the physiological capacity to disperse many kilometers (Botterweg 1982, Forsse and Solbreck 1985) and during outbreaks they are very abundant. For such a species, we expect no effect of small-scale connectivity. Nevertheless, we found a positive effect within a few hundred meters, and there may be at least two reasons for this: a critical attack density that is required for overcoming tree defenses and conspecific attraction (Mulock and Christiansen 1986, Nelson and Lewis 2008). The occurrence of a critical attack density strengthens the positive effect of connectivity on colonization probability, since there will more often be too few immigrating individuals at longer distances to initiate successful colonizations (Schippers et al. 2011). Conspecific attraction may also decrease colonization distances, by promoting migrants to nearby sites where conspecifics are already present (Weslien and Lindelöw 1990, Grevstad and Herzig 1997).

### Extinctions

Our results showed that during outbreaks, local extinction probabilities of bark beetles (i.e., the absence of current-year-killed trees in a pixel that was occupied the previous year) may be high, which agrees with studies of other bark beetle species (Hedden and Billings 1979, Colombari et al. 2013). The extinctions are most likely not deterministically caused by local host tree depletions, since the average spruce volume in occupied pixels was much higher than the mean volume of killed trees in the occupied pixels (in 2008: 158.2 $m^3 \cdot ha^{-1}$ and 6.2 $m^3 \cdot ha^{-1}$, respectively). Instead local extinction seems to be a rather stochastic process that was mainly explained by focal pixel characteristics, but somewhat also by connectivity and the composition of the surrounding landscape. It was negatively related to the size of the local population in the previous year, in accordance with two previous studies of the spruce bark beetle (Hedgren et al. 2003, Eriksson et al. 2008) and a generally high probability of small populations to go extinct due to demographic and environmental stochasticity (Lande 1998). For tree-killing bark beetles, environmental stochasticity is most likely much more important than demographic stochasticity in this respect, as extinction risks are probably high even for populations so large that demographic stochasticity has no significant impact, due to that many individuals are needed for successful attacks. At higher local population densities, beetles are able to initiate successful colonization also in trees with higher defense capacities (Boone et al. 2011), which means that large populations are less sensitive to the environmental stochasticity. The extinction probability decreased with increasing spruce volume in the focal pixel, which can be explained by the factors assumed to be responsible for the positive effect on colonization probability (see above).

In one year, more spruce in the surrounding forest increased the extinction probability. This effect could be because the immigration rate decreases when conditions in the surrounding landscape are more suitable for the migrating beetles. Studies of bark beetles (Powell and Bentz 2014) as well as other insects (Ovaskainen et al. 2008) lend support to this explanation, since they have shown that improvements in habitat quality in the surrounding landscape may decrease immigration rates to focal habitat patches. However, there are also many examples of the opposite effect (Tscharntke and Brandl 2004). The effect of spruce contributes to some extent to the patchy distribution pattern of the spruce bark beetle, since it counteracts the accumulation of large populations in those parts of the landscape with the highest spruce densities.

## CONCLUSIONS

We conclude that local populations of tree-killing bark beetles during outbreaks can be small, scattered across the landscape and have a high turnover. Local factors explained more of the colonization and extinction probability than the connectivity to occupied pixels and the tree composition of the surrounding landscape. Two reasons for the patchy and highly dynamic distribution of the bark beetles are the increased probability of successful attacks when exceeding a critical attack density and the fragmented distribution of large spruce volumes throughout the forest landscape. Of the occupied pixels, 81–87% had a volume of spruce of >100 $m^3 \cdot ha^{-1}$, although pixels with such large volumes of spruce only comprise 28% of the entire landscape.

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